HAWAI'I'S TERRESTRIAL ECOSYSTEMS PRESERVATION AND MANAGEMENT

Edited by
Charles P. Stone and J. Michael Scott

KAHA KA ʻIO KA MALIE,
E HOʻI PAHA KA ʻIO LANI
I KEIA MAU ʻAINA NEI
A KELA MANAWA
E ʻONIPAʻA KAKOU A PAU

The hawk soars in the calmness;
Perhaps the hawk's majesty will return
To the lands here.
Until that time,
We strive toward that goal.

Hawai'i's Terrestrial Ecosystems: Preservation and Management

Proceedings of a Symposium held June 5-6, 1984
at Hawai'i Volcanoes National Park

Edited by
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with Assistance of
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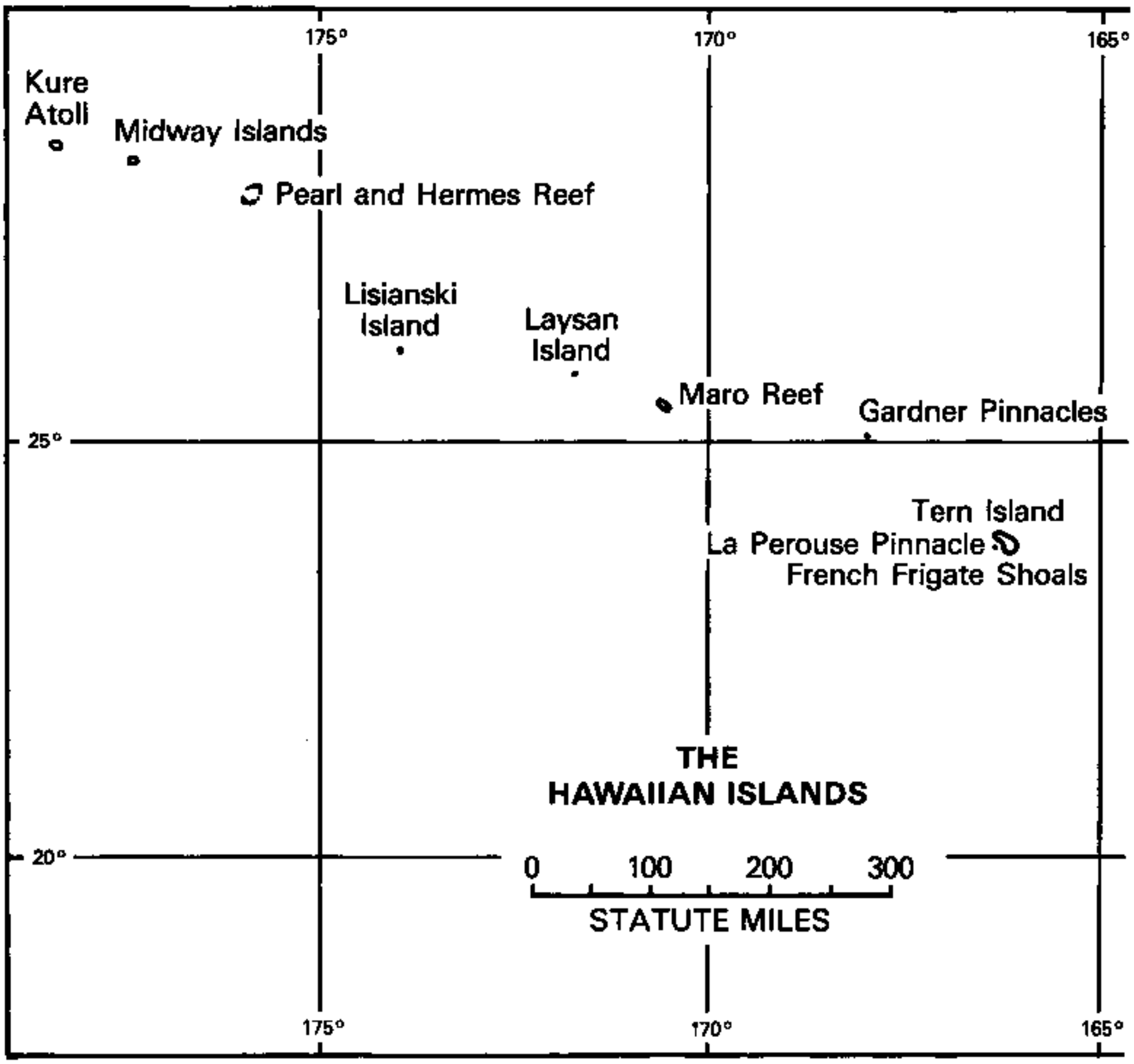

175°
170°
165°
Kure Atoll
Midway Islands
Pearl and Hermes Reef
Lisianski Island
Laysan Island
Maro Reef
Gardner Pinnacles
25°
Tern Island
La Perouse Pinnacle
French Frigate Shoals
THE HAWAIIAN ISLANDS
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175°
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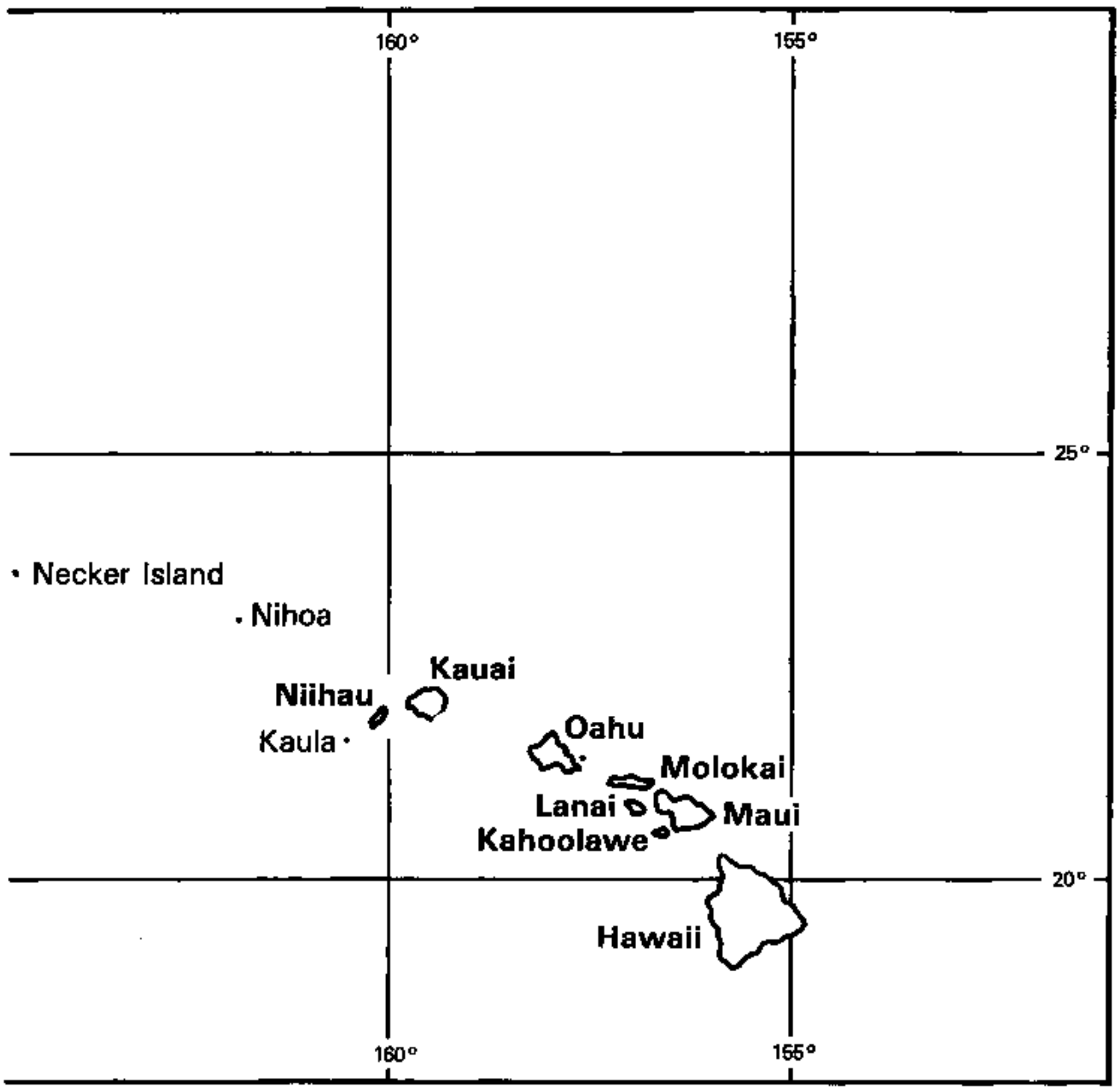
160°
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Necker Island
Nihoa
Kauai
Niihau
Kaula
Oahu
Molokai
Lanai
Maui
Kahoolawe
Hawaii
160°
155°

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FOREWORD

In the late 1950's, when this writer first plunged into Hawaiian wildlife management, life was so simple. "Ecosystems" were discussed mostly by professors of biology at the University of Hawai'i. Occasionally, a visiting scientist would pursue his specialty in our forests and prepare a paper on the importance of protecting the "unique Hawaiian biota." Few listened. Government agencies were primarily concerned with watershed protection to assure irrigation for agriculture, and with promoting commercial forestry, developing large State parks, and preventing the extinction of large, obvious endangered species (the nene). Citizen perception of natural resource management was that it should lead to consumption or use. Zoologists, botanists, malacologists, entomologists, and wildlife biologists, for the most part, were seen as oddball specialists with selfish professional motives.

Today, the word "ecology" is on the lips of average citizens, reporters, transients, and politicians. (In the 1960's, a local Honolulu candidate for office paraded a sign by the side of the road touting his primary qualification as an "ecologist".) Specialists in the fields of mammalogy, water resources, arachnidology, ornithology, and terrestrial ecosystems now abound in our institutions. Environmental protection as a concept permeates our Constitution, statutes, ordinances, rules, regulations, and policies. Citizen societies for the preservation of the treasures of nature have proliferated, and their representatives crowd the legislative hearing rooms. Natural scientists are honored by appointment to advisory boards and are inundated with Environmental Impact Statements to review. Things have become very complex.

With an enormous increase in our fund of information about native ecosystems, the lists of endangered species have grown longer, and a developer can barely move without stirring up a bee's nest of protest. New demands are being made upon the land, battering against the walls of preservation zoning. Ordinary people are beginning to see their lives affected by insect infestations, contaminated water supplies, and crowded wilderness areas. The first terrestrial ecosystem recognized by the State government in the form of a regulation to protect it was the Alaka'i Wilderness Preserve on Kaua'i in 1964. Since then, the Natural Area Reserve System has gobbled up the best parts of several State forest reserves. Other pieces of relatively native biotic complexes have been declared wildlife or plant sanctuaries, Nature Conservancy preserves, and expansions of National Parks.

Confrontations (not yet violent) have developed between academia, managers, administrators, and special interest groups over the use (or non-use) of our wild lands. Each group tends to perceive things in a vacuum of idealism or inertia. Strange as it may seem, however, a hunter can find common ground with a vertebrate zoologist, given a proper forum and time to communicate. (I have actually seen it happen!) That is why symposiums such as this one on "Hawai'i's Terrestrial Ecosystems: Preservation and Management" are so important. This is especially so if invited guests and speakers include bureaucrats, middle-level managers, educators, and interested citizens, and the forum allows time for discussion. For too long biologists have talked only to their own professional kin about the problems affecting our native biota. Government representatives are often too busy with budgets, legislative testimonies, and staff meetings to attend symposiums which expound upon the plight of our beasties and hibiscadelphuses.

A new trend in scientific gatherings has emerged in recent years. Heretofore, most "papers" were couched in classical formats, drawing weighty conclusions based on the formula of: data = hypothesis = experiment = theory = principle. Now the question is being added, "So what?" "Recommendations for management" now often appear in discussions at the end of journal articles.

The present Symposium not only revealed some of Mother Nature's most intimate secrets, but included discussions on what's wrong with her garden and pets, and suggested all of us get our act together to help her out. The sessions included consideration of conservation strategies, recovery potential, preserve design, management-research coordination, agency roles, legalities, incentives, cooperative planning, and costs. Tools of terrestrial ecosystem preservation were laid on the table as well. Look for repeated recommendations on restricting alien importations, and on active management (as well as preservation), biological control, research, and public education. Administrators and managers had their day in court and provided insights into the realities of politics, budgets, priorities, and legal constraints.

This book should be read with a sense of wonder that a common ground was found upon which no blood was spilled. It bodes well for the practical solution of our most acute terrestrial ecosystem problems.

Honolulu, Hawaii
1985

R.L. Walker

PREFACE

The wonders of nature, as manifested through the processes of natural selection and evolution, are nowhere better demonstrated than on the islands of the Hawaiian archipelago. Some of the rarest and most unique life-forms found anywhere have been fostered by the "splendid isolation" of the place; yet the ecosystems of the Islands also lack much of the resilience that characterizes continental systems partly for this reason. The introduction of man, goats, pigs, Myrica faya, Andropogon, mongooses, rats, Japanese white-eyes, mosquitoes, and a whole host of additional alien creatures has dramatically disturbed ecosystem structure and function.

Hawai'i National Park, established on August 1, 1916, gave official national recognition to the uniqueness found in Hawai'i. International recognition was offered what are now Hawai'i Volcanoes and Haleakala National Parks in 1980, when they were designated the Hawaiian Islands Biosphere Reserve by the Man and the Biosphere Program of the United Nations Educational, Social and Cultural Organization (UNESCO). Yet such recognition has obviously not prevented the biological disturbances widespread throughout most of Hawai'i.

In the late 1960's, the National Park Service began to deal with the problem of invasion and degradation of unique ecosystems by alien plants and animals. Managers responsible for protecting native park ecosystems and researchers who had some knowledge of how ecosystems functioned gradually developed a strong cooperative bond. The manager wanted to do his job effectively and realized the need for accurate information to do so. The researcher soon learned that the scientific literature, though important, was not the best way to communicate knowledge to resource managers. Direct one-on-one dialogue developed. Indeed, nowhere in the Park Service has more time been spent in direct communication among researchers and resource managers in the past 15 years, than in the Hawaiian parks. Although problems in the cooperative approach have arisen and both groups have been frustrated by lack of sufficient funding to do adequate jobs, dynamic and practical programs have arisen, and considerable progress in resource protection and management is being made.

In addition to the dedication and hard work of concerned citizens inside and outside the parks, I believe that two factors have contributed to Park Service success in this area. One important development was increased focus on natural resource research in Hawai'i through establishment of the Cooperative Park Studies Unit at the University of Hawai'i (CPSU/UH) on March 16, 1973. The CPSU provided a continuous administrative presence on the campus, reduced overhead on contracts, established a technical report series for getting research reports to managers, provided a professional extension function for managers needing consultative assistance, and essentially made every university faculty member and graduate student on the UH campus an adjunct member of the Park Service staff in Hawai'i, available on call when needed but costing the Service nothing the rest of the time. The selection of C.W. Smith as CPSU Unit Leader in August 1975 marked an important step in the CPSU/UH's rise to prominence as the most successful and productive CPSU in the Park Service. I predict that the Unit will be more widely used for the benefit of Hawaiian natural resources in the future.

A second development, in July 1976, was the First Natural Science Conference. Held in Hawai'i Volcanoes National Park, it opened a new horizon of communications between research and resource managers in Hawai'i. Attendance by researchers, as well as administrators, resources managers, and educators, from diverse organizations and agencies has increased with each conference. A special 2-day symposium entitled "Preservation and management of terrestrial Hawaiian ecosystems" was an outgrowth of the 5th Natural Science Conference in 1984, and it represents another milestone in the maturation of the communication process between natural resource researchers and managers. A common theme that came through time and again in this Symposium was the continued need for a close working relationship between researchers and resource managers. This has long been a strong point in Hawaiian parks, but like any higher degree of social order, it takes continued effort and expenditure of energy to maintain.

It is a self-evident truth that ecologically we are all joined together in life on the planet Earth. Perhaps nowhere is this fact more evident than in

Hawai'i. The strongly insular nature of Hawaiian evolutionary history, the limited resources of island communities, and the magnitude of current threats from alien species including man make it absolutely imperative that we combine efforts to preserve near-natural ecological processes. When scientists, administrators, and resource managers from the National Park Service, U.S. Forest Service, U.S. Fish and Wildlife Service, Hawai'i Department of Land and Natural Resources, Hawai'i Department of Agriculture, University of Hawai'i, B.P. Bishop Museum, The Nature Conservancy, and Pacific Tropical Botanic Garden can spend 2 days of intensive, in-depth discussions on matters of common concern, one can only be encouraged about the future of Hawaiian ecosystems.

This book represents an important written record of the 2-day Symposium. It is a state-of-the-science document that summarizes the latest and best information available for managing natural resources in Hawai'i and reports social, political, and cultural aspects of conservation issues. The implications are not limited to national parks or to Hawai'i, but have applications for many situations where natural resources are limited and fragile, and conflicts in use diverse. The valuable interagency cooperation represented by this volume is a positive indication of hope for eventual success in solving many of the difficult problems we face in preserving ecological processes and systems in Hawai'i.

College Station, Texas D.B. Fenn
1985

ACKNOWLEDGEMENTS

The Symposium that resulted in the publication of this volume was conceived early in 1983 and seems to have grown "like Topsy" ever since. The care and feeding of such an important and demanding child would not have been possible without numerous helpers-at-the-nest and foster parents. We would like to especially thank our supervisors H.R. Perry, Jr., and D.B. Fenn for allowing us the latitude to organize and host the meeting and finalize the results in writing. Support for publication was provided by the National Park Service and the U.S. Fish and Wildlife Service.

The excellent work of the contributing authors and session chairpersons is of course the basis for the volume. We appreciate having the chance to work closely with so many unique personalities and watching manuscripts take shape in so many different ways. We are especially grateful for their underlying professional attitudes and support for our efforts to bring it all together.

We want to express special appreciation to those who contributed to the fourth session so ably summarized by C.B. Kepler. We decided not to print their presentations, because some were not submitted in writing, and also because we believed that some of the ideas generated could be discussed more fully in a final chapter. These people provided tremendous stimulation at the meeting and to us; they are credited as contributors and also listed in C.B. Kepler's summary.

Individuals on each of our staffs contributed in numerous ways, and include J. Jacobi, J. Williams, S. Mountainspring, S. Doyle, R. Sugihara, P. Higashino, S. Anderson, A. Kikuta, D. Espy, D. Stone, L. Cuddihy, L. Chow, and S. Graves. Their cheerful tolerance of our absences and preoccupation with the ideas, meetings, editing, and publishing is much appreciated.

We would like to thank the Superintendent of Hawai'i Volcanoes National Park, D.B. Ames, for his support and for sharing his Administration, Resource Management, Protection, Maintenance, and Interpretation staff where needed to facilitate the meeting. Staff of the Hawai'i Natural History Association also helped.

The Director of the Cooperative National Park Resources Studies Unit at the University of Hawai'i, C.W. Smith, was his usual extremely helpful self in providing publicity for the meeting, advice on editing and publication, a mechanism for handling funding, and assistance with some of the typing. We agree with D.B. Fenn, that the CPSU at the University of Hawai'i is the best and most productive in the National Park Service.

The artists who contributed their works and thereby enhanced the attractiveness of the written words herein are D. Varez, R.L. Walker, H.D. Pratt, D.B. Stone, R. Hazlett, and G.B. Harry. The photo for the frontispiece was contributed by R.J. Shallenberger, and the Hawaiian proverb was provided by S. Gon III.

Assistance with indexing was provided by P. Lockwood, C. Sodetani, and B. Carr. K. Bridges of the University of Hawai'i allowed us use of his personal laser jet printer and helped with computer problems. We are grateful for the time he took from his busy schedule to share his knowledge and equipment with us.

The people of University of Hawai'i Press and especially Janet Heavenridge, Design and Production Manager, were very helpful to us during all stages of the publishing process (including what seemed like periods of acute lack of progress on our part). They gave us considerable good advice on the mechanics of preparing a book, many examples of how other books had been handled, and encouragement. And Jan gave of her time and effort even before she saw the color of our money--which was just over the horizon for a long, long time.

We appreciate the willingness of J.O. and S.P. Juvik, Department of Geography, University of Hawai'i/Hilo, to review the entire volume for cohesiveness, usefulness, and errors in fact. The length and diversity of the contributions made this task especially difficult. Authors and editors, of course, are responsible for what appears herein.

Although they are acknowledged on the title page, the efforts of Danielle B. Stone and April R. Komenaka in helping us bring this project off deserve additional mention here. Not only did these women serve as two extra sets of eyes and ears to help correct the grammar and punctuation of our wayward child and try to teach consistency in all things (especially literature citations), they remained enthusiastic and good-humored while doing so and went well beyond their job descriptions in challenging us to produce our best efforts.

And, last (as traditionally is done so that people will read through the acknowledgements to the end to find out their names and how they are recognized), we thank our wives Danielle and Sharon for willingly supporting us in what we hope is a milestone in Hawaiian biology. Danielle was deeply involved in editing and word processing all of the papers and put a great deal of her own valuable time into the effort. She also was an excellent sounding board for biological ideas for one of us (cps). Both women provided understanding, warm, and loving environments in which to produce, despite major changes in their own lives, including a move to California for the Scotts. They both deserve mahalo nui loa (deep thanks) from those who find this volume useful.

C.P. Stone
Hawai'i National Park, Hawai'i
1985

J.M. Scott
Ventura, California

EXPLANATORY NOTES

Budgetary constraints made typesetting of the entire book impossible. Thus, camera-ready copy prepared on word processor and laser jet printer was submitted to the University of Hawai'i Press. Unfortunately, it was not possible to include macrons and other diacritics with the software used. The Chicago Manual of Style (13th edition) was our reference for the most part, but sometimes we established our own guidelines to enhance consistency.

Geographic, taxonomic, and subject indexes, together with an expanded table of contents, should help the reader find most subjects of interest. A key-word, rather than interpretive, index approach was used for subjects, so the reader may need to scan the topics key-worded for best results.

Because of inconsistencies in use of capitals, punctuation, and diacritics in literature citations (by publishers, original authors, and Symposium authors), and because we did not have adequate time or resources to check all citations, we adopted a uniform approach in punctuation and capitalization of titles. This necessarily resulted in some differences with some original titles, and the original source should be consulted if this is of concern.

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I. STATUS, RESEARCH, AND MANAGEMENT NEEDS OF THE NATIVE HAWAIIAN BIOTA

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below approximately 500 m elevation, or large upland areas which were generally devoid of native vegetation. The unsampled areas included much of the Waimea plain between Laupahoehoe and Waimea. We also did not survey large portions of the Pohakuloa Training Area in the saddle between Hualalai, Mauna Loa, and Mauna Kea volcanoes, although these areas do contain some large areas of native dry forest and scrub.

Vegetation Mapping

The vegetation maps produced during this project display the existing plant communities based on both species composition and vegetation structure. At the most detailed level (Level 3), the map units reflect 4 major components of the vegetation: 1) tree canopy crown cover, 2) tree canopy height, 3) tree species composition, and 4) dominant understory species composition. The understory category is chiefly represented by regularly repeating species groups in different habitat types. At the most detailed level, 369 vegetation units were identified for the area mapped on the island of Hawai'i alone. Of this total, 137 of the detailed units constituted 90% of the area mapped.

Although the detailed vegetation maps are useful for intensive field studies of specific areas, there are too many units to deal with at this level when large portions of the Island are considered. To allow for a more usable island-wide perspective, the detailed map units were grouped into a hierarchical classification that reflects an increasing degree of generalization of the structural and floristic characteristics of the vegetation. In this classification, the 369 Level 3 map units were first grouped into 81 more general Level 2 units, which, in turn comprise 17 Level 1 units.

The most general map units (Level 1) represent a generalized reconstruction of the original vegetation in the areas surveyed, as they might now be without the effects of disturbance by man or his introduced species. These reconstructed units were used in assessing the present status of the vegetation as mapped for the study area at Level 2. The Level 2 units, which represent actual vegetation components identified in the field, are grouped under the Level 1 units according to the degree of disturbance (as indicated by dominance of native or introduced species) of the overstory or understory components of the vegetation. For this classification, the tree component was considered the dominant layer if it had more than 25% crown cover (i.e., open or closed forest).

Four disturbance categories were distinguished in this system: 1) NN = communities totally dominated by native species of plant (e.g. certain wet forest, many alpine areas); 2) NX = communities which have the subdominant vegetation layer predominately occupied by exotic species (e.g. closed canopy koa-'ohi'a (Acacia koa-Metrosideros polymorpha) forest with a grazed, mixed-grass understory); 3) XN = communities dominated by introduced species, but containing remnant populations of native species; no native community structure remaining (e.g. many lowland dry forest communities); 4) XX = communities totally dominated by introduced plants; almost no native species remaining (e.g. agricultural lands, urban areas).

Assessment of Status of Native Vegetation

An initial assessment was made of the status of the different vegetation units within the HFBS study area, by breaking down the area of each Level 1 unit into 4 component disturbance categories. By this means, a Level 1 unit which had the majority of its area mapped as still dominated by native species of plants (NN) would be considered to be in relatively good condition. There is an obvious problem in this approach, in that certain native-dominated vegetation types, such as early seral communities, have a relatively limited species composition and structure. However, other units, such as low elevation dry or mesic communities, may be severely disturbed overall, but have a large number of rare plant species in remnant populations. These examples emphasize the need to consider both the degree of disturbance of the structure of the community and the species complement which is still or previously found in that unit. One additional limitation is that only the areas sampled during the HFBS were considered in the analysis reported in this paper. The rest of the Island not covered during this survey originally did, and in some areas still does, contain native-dominated communities. This problem does not seriously affect the assessment of the distribution and current status of forest bird habitat on the island of Hawai'i, since nearly all habitats containing, or potentially containing, native forest birds were included in the survey. However, it does limit a realistic assessment of low elevation vegetation.

Analysis of Endangered Species Data

To streamline the discussion throughout the rest of this paper, we have used the term "endangered species" to include not only the presently listed endangered or threatened species of Hawaiian plants and animals, but also the Category 1 candidate endangered species of plants. This rationale is based on the expectation that eventually most candidate species will be officially designated as either endangered or threatened.

The information on endangered species of native forest birds and plants used in this analysis was also collected during the HFBS. For the purpose of the present paper, we have only dealt with individual endangered species on a presence-absence basis within particular vegetation units, although more detailed information was collected for both groups, particularly the birds. Here we address "rare species richness" within individual vegetation types (i.e. comparisons of vegetation units based on aggregations of endangered or threatened species). This approach allows the identification of vegetation units with several species of interest in common.

RESULTS

Current Status of Major Native Vegetation Units

On the island of Hawai'i the HFBS covered nearly 500,000 ha of the total area of the Island. Within that sampling universe, 17 Level 1 vegetation types were identified (table 1). The 3 "Unassigned Units" included in this table represent former native plant communities which have been so degraded that they could not easily be assigned to one of the other reconstructed vegetation categories. The largest unit sampled was the wet 'ohi'a forest which covered approximately 100,000 ha, or 20.5% of the total area. The smallest unit mapped was the wet, open bog community (28 ha). Over 11% (55,176 ha) of the study area was classified as "Not Vegetated."

The wet 'ohi'a forest (unit 32) occurs in the study area between approximately 500 m and 1,700 m elevation on the windward side of the Island and to 1,500 m in wet leeward areas. Just above this vegetation type, either the mesic 'ohi'a (unit 22) or mesic koa-'ohi'a forest (unit 21) is found, depending on the age and type of substrate. In some areas above the mesic communities a mountain parkland community occurs, comprised of a mixture of koa with mamane (Sophora chrysophylla) stands, native scrub, and grassland (unit 13). The highest elevation tree community on Mauna Loa is primarily dry subalpine scrub 'ohi'a (unit 19), but on Mauna Kea dry mamane (unit 16) or mamane-naio (Myoporum sandwicense) woodland (unit 15) predominates. Above treeline on all 3 tall volcanoes (including Hualalai), a dry alpine scrub community (unit 18) is found, composed chiefly of the shrubs Vaccinium spp., Styphelia tameiameiae, and Dodonaea viscosa with mixed grasses.

The mesic pioneer scrub (unit 24) and the tall wet 'ohi'a forest with a native shrub-matted fern understory (unit 33) represent early and slightly older seral stages of vegetation development on recent volcanic substrates in wet habitat. The 'ohi'a dieback

Table 1. List of the 17 reconstructed vegetation units in the HFBS study area on the island of Hawai`i.

#	Map Symbol	Description of Unit	Area (Ha)
18	D:(ns)	Dry native shrub community	6,715
19	D:(ns)Me	Dry native shrub community with scattered `ohi`a trees	35,231
11	D:Ac-Me-nt(ns-ng)	Dry koa-`ohi`a forest with a native shrub-grass understory	4,Ø61
13	D:Ac-So(ns-ng)	Dry koa-mamane forest with a native shrub-grass understory	3Ø,1Ø7
14	D:Me,nt(ns)	Dry `ohi`a forest with a native shrub understory	63,383
15	D:My-So(ns-ng)	Dry naio-mamane woodland with a native shrub-grass understory	12,Ø12
16	D:So(ns-ng)	Dry mamane woodland with an native shrub-grassland understory	28,424
17	D:nt(ns)	Dry mixed native trees forest with a native shrub understory	5,933
1Ø	D:UNASSIGNED	Dry habitat - unassigned units	1Ø,265
24	M:(ns) pio	Mesic pioneer native shrub community	2,775
21	M:Ac-Me,nt(ns)	Mesic koa-`ohi`a forest with a native shrub understory	39,3Ø3

Table 1. Continued.

#	Map Symbol	Description of Unit	Area (Ha)
22	M:Me,nt(ns)	Mesic `ohi`a forest with a native shrub understory	35,361
23	M:nt(ns)	Mesic mixed native trees forest with a native shrub understory	75
20	M:UNASSIGNED	Mesic habitat - unassigned units	10,946
36	W:(bg)	Wet open bog community	28
35	W:(ns/mf)Me,nt [dieback]	Wet native shrub-matted fern community with scattered `ohi`a trees (dieback)	6,204
31	W:Ac-Me,nt(tf-ns)	Wet koa-`ohi`a forest with a treefern-native shrub understory	34,730
33	W:Me,nt(ns/mf)	Wet `ohi`a forest with a native shrub-matted fern understory	11,123
32	W:Me,nt(tf-ns)	Wet `ohi`a forest with a treefern-native understory	101,824
30	W:UNASSIGNED	Wet habitat - unassigned units	1,777
	NOT VEGETATED		55,176
		TOTAL AREA =	495,454

unit (35) is another successional unit which developed in response to natural and widespread periodic canopy tree defoliation or death in the mature wet 'ohi'a forest (Mueller-Dombois 1980; Jacobi 1983b). One other wet habitat vegetation type is the open bog community (unit 36). There are relatively few open bogs on the island of Hawaii, and they are generally scattered throughout the montane wet forest on relatively old ash substrates.

The restriction of the HFBS study area to current or potential native forest bird habitats resulted in an undersampling of certain vegetation types, some of which are known to have been quite extensive at lower elevations. These units included lowland wet forest (below 500 m elevation) and particularly dry mixed forest (unit 17) and mesic mixed forest (unit 23), recognized as originally being among the richest of the native plant communities (Rock 1919). Our study area included only 5,933 ha and 75 ha of dry mixed and mesic mixed, respectively. Two other units we did not sample were the mesic coastal lowland forest and the coastal strand.

The present condition of the native vegetation within the study area is summarized in table 2. It must be emphasized that the percentage values given in this table for the 4 disturbance categories in the different vegetation units reflect a summary for only the area sampled during the HFBS. Additionally, the percentages in each class for some of the units could actually be lower than reported if the "Unassigned Units" are eventually assigned to them.

The 6 vegetation types in group A of table 2 still appear to be in relatively good condition, based on the percentage of area dominated by native species (Category NN). All but one of the wet habitat communities mapped are included in this group of relatively undisturbed units. The other 2 members of Group A are the subalpine scrub community (Unit 19) and the mesic pioneer scrub community (unit 24).

The second group identified in table 2 includes most of the mapped mesic and dry units, plus the open bog community. Two units, the dry 'ohi'a forest (unit 14) and the mesic 'ohi'a forest (unit 22), still had nearly half of their total area mapped as native-dominated at the time of the survey. Of the remaining members of this group, 6 units had no mapped area still totally dominated by native species, although several of them had significant portions in the partly disturbed category (NX).

Table 2. List of the 17 reconstructed vegetation units in the HFBS study area, with a summary of percentage of total area in each of the 4 disturbance categories and the number of endangered or candidate endangered birds and plants for each unit.*

	Unit #	Map Symbol	Area (Ha)	Disturbance Category (%)**				Endangered	
				NN	NX	XN	XX	Birds	Plants
A. Units with large portions still dominated by native species									
	19	D:(ns)Me	35,231	100.0	-----	-----	?	3	1
	24	M:(ns) pio	2,775	100.0	-----	-----	-----	2	--
	35	W:(ns/mf)Me,nt [dieback]	6,205	98.5	1.4	-----	?	1	--
*	31	W:Ac-Me,nt(tf-ns)	34,730	94.3	5.6	-----	?	5	9
	33	W:Me,nt(ns/mf)	11,123	100.0	-----	-----	?	-	1
*	32	W:Me,nt(tf-ns)	101,824	91.5	4.4	4.0	?	6	11
B. Units with greatly reduced or no area totally dominated by native species									
	18	D:(ns)	6,715	-----	100.0	-----	?	1	--
	11	D:Ac-Me-nt(ns-ng)	4,061	-----	34.1	65.8	?	1	1
*	13	D:Ac-So(ns-ng)	30,107	-----	33.8	66.1	?	4	2
*	14	D:Me,nt(ns)	63,383	56.4	14.2	29.3	?	4	9
*	15	D:My-So(ns-ng)	12,012	7.9	64.1	27.8	?	2	3
*	16	D:So(ns-ng)	28,424	-----	47.8	52.1	?	4	2

Unit #	Map Symbol	Area (Ha)	Disturbance Category (%)** NN	NX	XN	XX	Endangered Birds	Plants
* 17	D:nt(ns)	5,933	-----	21.4	78.5	?	1	6
* 21	M:Ac-Me,nt(ns)	39,303	13.4	69.3	17.2	?	6	11
* 22	M:Me,nt(ns)	35,361	45.1	42.6	12.2	?	6	2
23	M:nt(ns)	75	-----	100.0	-----	?	--	--
36	W:(bg)	28	12.0	52.6	35.3	?	--	1
C. Highly disturbed areas, few native species remaining								
10	D:UNASSIGNED	10,265	-----	-----	0.8	99.1	--	--
20	M:UNASSIGNED	10,946	-----	-----	1.2	98.7	1	--
30	W:UNASSIGNED	1,777	-----	-----	-----	100.0	1	--
	NOT VEGETATED	55,176	-----	-----	-----	-----	--	--

* Units marked with an asterisk (*) had a relatively large number of endangered species recorded during the HFBS.

** NN = communities totally dominated by native plants.
NX = communities with subdominant vegetation layer primarily introduced plants.
XN = communities dominated by introduced species but containing remnant populations of native plants.
XX = communities totally dominated by introduced plants.

The third category in table 2 contains the 3 highly disturbed "Unassigned Units" in each habitat and the large "Not Vegetated" map unit. The unassigned units combined represent less than 5% of the total area surveyed.

Summary of Endangered Species Found Within Study Area

All 7 of the endangered terrestrial forest birds and 33% of the endangered or candidate endangered plants (42 of 129) from the island of Hawai'i were recorded at least once during the HFBS. The relatively low percentage of endangered plants encountered reflects: 1) the fact that the survey was focused on endangered forest birds and therefore did not include large portions of potential endangered plant habitat, particularly below 500 m elevation, and 2) the sampling framework used (transects established at 3.2 km intervals) was too coarse to adequately sample rare plant populations. Despite these limitations, the systematic information gathered on endangered plants during the survey allows a general overview of the distribution of some rare plants found within the study area.

The numbers of species of endangered birds and plants encountered in each of the Level 1 map vegetation units are listed in the last 2 columns in table 2. At least one endangered bird or plant species was recorded in every vegetation unit sampled except the mesic mixed native tree community (unit 23). As mentioned earlier, this large and extremely species-rich unit was barely sampled during our survey. In fact, a large number of endangered plants are known from this vegetation type (Wagner, Herbst, and Yee, this volume). The endangered bird listed for the unassigned wet and mesic units is the Hawaiian hawk or 'io (Buteo solitarius), which has an extremely broad distribution, including some highly modified habitats.

The 9 vegetation types marked with an asterisk (*) in table 2 had a relatively large number of endangered species recorded in them during the survey. Two of the species-rich units, the wet koa-'ohi'a forest (unit 31) and the wet 'ohi'a forest (unit 32) are included in group A of table 2. However, a more detailed analysis of the HFBS bird data set revealed that most of the endangered forest bird populations were found at greater than 1,500 m elevation (Scott et al., in press; Scott, Kepler, and Sincock, this volume). Only approximately 25% of the wet 'ohi'a forest and less than 20% of the wet koa-'ohi'a forest was found above 1,500 m. The rest of the species-rich vegetation types are in the more heavily disturbed group B. One of the most important units of group B is the mesic koa-'ohi'a forest (unit 21) which had 6 endangered birds and 11 endangered plants recorded in it. However, only 13.4% of this unit was mapped as native-dominated.

DISCUSSION

Factors Responsible for Degradation of Native Habitats

The most rapid changes to native communities have resulted from direct human activities such as agriculture, urbanization, logging, etc. The majority of habitat loss from land conversion for strict agricultural practices and urbanization has occurred below 1,000 m elevation. Recent evidence has also indicated that many of the lower elevation communities were severely modified by the Hawaiians prior to western contact (Kirch 1982). Most of the recent expansion of "urbanization" in still native habitats has been in the form of new housing developments, e.g. in the Volcano and Kona regions on the island of Hawai'i.

Logging activities have primarily been concentrated in the upper elevation mesic koa-'ohi'a forest. Koa is recognized as an exceptionally fine cabinet wood and is always in high demand. Following logging, a usual practice has been to convert the newly opened forest to ranchland by introducing both cattle (_Bos taurus_) and pasture grasses to the area. A detailed analysis of the HFBS data has shown that this combination of opening the tree canopy by logging and elimination of the understory by cattle results in significantly reduced quality habitat for forest birds (Scott et al., in press). Similar effects have been documented for some of the rare native plant species such as _Vicia menziesii_ (Warshauer and Jacobi 1982).

Fire is another disturbance factor which can rapidly change the structure and composition of the native vegetation, particularly in the dry and mesic habitats. The history of fire in the natural Hawaiian ecosystem has received only limited attention (Vogl 1969). On the 2 youngest islands, Maui and Hawai'i, natural fires can still occur as the result of volcanic eruptions or rarely from lightning strikes. However, most of the recent fires in the Islands have been caused by man. In 1977, an accidentally started fire burned a significant portion of the mamane-naio woodland on Mauna Kea on the island of Hawai'i (Scott et al. 1984). This habitat is the only remaining area where the endangered palila (_Loxioides bailleui_) is found.

The most widespread disturbances to the native communities have resulted from the effects of the numerous species of both plants and animals introduced into Hawai'i by man. Particularly damaging have been the large feral mammals including cattle, goats (Capra hircus), sheep (Ovis aries), pigs (Sus scrofa), and deer (Odocoileus hemionus and Axis axis). A small, but significant, proportion of the nearly 4,500 taxa of introduced plant species is recognized as being particularly damaging to the native habitats (Smith, this volume). Once established, species like fountain grass (Pennisetum setaceum) and Koster's curse (Clidemia hirta) cover large areas, replacing nearly all of the native ground layer species. Introduced vines such as Passiflora mollissima have the potential to drape tall koa trees and eventually break down the tree canopy with their weight (Warshauer et al. 1983).

Recovery Potential for Damaged Native Ecosystems

Despite what may appear as almost insurmountable pressures from the numerous habitat degradation factors, several of the native plant communities have the capacity for significant recovery if some of the detrimental factors are controlled. The review of exclosure studies in Hawai'i presented by Loope and Scowcroft (this volume) shows that in many habitats, elimination of feral animals alone will produce positive results to native vegetation. The greatest potential for habitat restoration appears to be in those communities above about 1,000 m elevation that still retain some degree of their original vegetation structure and composition (category NX in the earlier discussion in this paper). The only hope for the rehabilitation of units in the XN or XX disturbance categories would involve an intensive management program including large-scale replanting of key native components of the community. Even with this degree of manipulation, it is doubtful that widespread self-maintaining native communities could be reestablished.

Conservation Strategies

The maintenance of the greatest number of viable populations of the numerous endangered Hawaiian plants and animals appears to be best accomplished through the protection of relatively intact native communities. This approach seems to be valid for 2 reasons: 1) unnaturally rare species which evolved in a particular community would be expected to be most easily maintained there, and 2) many of the endangered species in Hawai'i are found to co-occur in certain community types. The management of a specific habitat for one endangered species should, in most cases, benefit other endangered species as well.

The development of a preserve system for the protection of endangered Hawaiian species should focus on securing and managing significant portions of those species-rich and threatened vegetation units identified in table 2 which are still dominated by native species. Management programs should also be developed to reduce or eliminate alien pressures in adjacent parcels to eventually supplement existing intact portions of these units. Specifically, it is essential that no more of the remaining 13.4% of the native-dominated mesic koa-'ohi'a forest be destroyed. Any further loss will likely result in the loss of some of the dependent endangered species. The upland portions of the wet koa-'ohi'a and wet 'ohi'a forests which are also important endangered bird and plant habitats should be protected from further degradation. Other vegetation units with extremely urgent protection and management needs are the lowland mesic and dry mixed forest, of which little remains.

We must be careful not to direct all of our attention toward trying to maintain extremely rare species in highly disturbed habitats, while other endangered species with reduced, but more substantial, populations continue to decline in abundance and distribution. This is not to say that we should totally ignore so-called "basket-case" species; instead, we need to focus more of our efforts on protecting rare species still within natural or nearly natural environments. This approach should not only be more cost-effective than attempting recovery of single species, but should reduce the number of endangered species of concern in the future. In the final analysis, the success of research and management efforts will be measured in the year 2050, not so much by the number of species saved from extinction, but by how many species were prevented from becoming endangered.

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LITERATURE CITED

Berger, A.J. 1981. _Hawaiian birdlife_. 2nd ed. Honolulu: Univ. Pr. Hawaii.

Carlquist, S. 1970. _Hawaii: a natural history_. Garden City, New York: Nat. Hist. Pr.

Carson, H.L. 1982. Evolution of _Drosophila_ on the newer Hawaiian volcanoes. _Heredity_ 48(1):3-25.

Fosberg, F.R. 1948. Derivation of the flora of the Hawaiian Islands. In _Insects of Hawaii_, ed. E.C. Zimmerman, Vol. 1, _Introduction_, 107-119. Honolulu: Univ. Hawaii Pr.

Fosberg, F.R., and D. Herbst. 1975. Rare and endangered species of Hawaiian vascular plants. _Allertonia_ 1:1-72.

Jacobi, J.D. 1983a. Mapping the natural vegetation of the Hawaiian Islands. Pres. 15th Pac. Sci. Conf., Dunedin, New Zealand, February.

Jacobi, J.D. 1983b. _Metrosideros_ dieback in Hawaii: a comparison of adjacent dieback and non-dieback rain forest stands. _New Zealand J. Ecol._ 6:79-97.

Kirch, P. 1982. The impact of the prehistoric Polynesians on the Hawaiian ecosystem. _Pac. Sci._ 36:1-14.

Loope, L., and P.W. Scowcroft. Vegetation response within exclosures in Hawaii: a review. [This volume]

Mueller-Dombois, D. 1980. The ohia dieback phenomenon in the Hawaiian rain forest. In _The recovery process in damaged ecosystems_, ed. J. Cairns, 153-161. Ann Arbor, Mich.: Ann Arbor Sci. Pub.

Mueller-Dombois, D., K.W. Bridges, and H.L. Carson, eds. 1981. _Island ecosystems: biological organization in selected Hawaiian communities_. Stroudsburg, Penn.: Hutchinson Ross Pub. Co.

Olson, S., and H.F. James. 1982. Fossil birds from the Hawaiian Islands: evidence for wholesale extinction by man before Western contact. _Science_ 217(4560):633-635.

Rock, J.F. [1913] 1974. _The indigenous trees of the Hawaiian Islands_. Reprint, with Introduction by S. Carlquist and Addenda by D.R. Herbst. Privately pub.

Rock, J.F. 1919. A monographic study of the Hawaiian species of the tribe Lobelioidae, family Campanulaceae. B.P. Bishop Mus. Mem. 7(2).

St. John, H. 1973. List and summary of the flowering plants in the Hawaiian Islands. Pac. Trop. Bot. Gard. Mem. 1.

Scott, J.M., J.D. Jacobi, and F.L. Ramsey. 1981. Avian surveys of large geographical areas: a systematic approach. Wildl. Soc. Bull. 9:190-200.

Scott, J.M., C.B. Kepler, and J.L. Sincock. Distribution and abundance of Hawaii's endemic land birds: conservation and management strategies. [This volume]

Scott, J.M., S. Mountainspring, F.L. Ramsey, and C.B. Kepler. In press. Forest bird communities of the Hawaiian Islands: their dynamics, ecology, and conservation. Stud. Avian Biol.

Scott, J.M., S. Mountainspring, C. van Riper III, C.B. Kepler, J.D. Jacobi, T.A. Burr, and J.G. Giffin. 1984. Annual variation in the distribution, abundance and habitat of the palila. Auk 101:647-664.

Smith, C.W. Impact of alien plants on Hawaii's native biota. [This volume]

U.S. Congress. 1973. Endangered species act of 1973. 93rd Congr., Dec.

U.S. Fish and Wildlife Service. 1980. Endangered and threatened wildlife and plants; review of plant taxa for listing as endangered or threatened species. Fed. Register 45(242):82480-82569.

U.S. Fish and Wildlife Service. 1983. Endangered and threatened wildlife and plants. Fed. Register 48:34182-34196.

Vogl, R.J. 1969. The role of fire in the evolution of the Hawaiian flora and vegetation. Proc. Ann. Tall Timbers Fire Ecol. Conf., April 1969, 5-60. Tallahassee.

Wagner, W.L., D.R. Herbst, and R.S.N. Yee. Status of the native flowering plants of the Hawaiian Islands. [This volume]

Warshauer, F.R., and J.D. Jacobi. 1982. Distribution and status of *Vicia menziesii* Spreng. (Leguminosae): Hawaii's first officially listed endangered plant species. Biol. Conserv. 23:111-126.

Warshauer, F.R., J.D. Jacobi, A. La Rosa, J.M. Scott, and C.W. Smith. 1983. The distribution, impact and potential management of the introduced vine Passiflora mollissima (Passifloraceae) in Hawaii. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. 48. Honolulu: Univ. Hawaii.

Zimmerman, E.C. 1948. Insects of Hawaii. Vol. 1, Introduction. Honolulu: Univ. Hawaii Pr.

2.

STATUS OF THE NATIVE FLOWERING PLANTS OF THE HAWAIIAN ISLANDS

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ABSTRACT

Estimates of the total number of native Hawaiian plants are widely divergent because of differences in species concepts; our evaluation suggests 1,200-1,300 native species. Hawai'i has the highest number of candidate threatened and endangered plants for the United States (31%), with approximately 10% of the native flowering plants already extinct. Although a modern taxonomic review of the Hawaiian flora will reduce the number of taxa considered valid, roughly 50% of the flora will still be considered threatened or endangered. Currently 11 Hawaiian plants are listed as endangered, one has been proposed as endangered, and the documentation for an additional 9 is currently under review.

An evaluation comparing the number of candidate taxa on each island and in each major ecological zone shows that the islands with the highest percentages of candidate taxa are O'ahu (27.3%), followed by Hawai'i (18.3%), Maui (16.8%), and Kaua'i (14%). The low numbers on islands such as Ni'ihau (1.5%) and Kaho'olawe (0.7%) are apparently partly a reflection of the loss of most of the native vegetation prior to study of these islands, and partly because of lower physiographic diversity. The ecological zones most severely degraded are mixed mesophytic forest, which harbors nearly 33% of the total candidate taxa, and low elevation rain forest with 24%. Not indicated by this analysis is the severe degradation of lowland vegetation (with 14% of total candidate taxa) and coastal vegetation (with 9.5%) that occurred prior to their scientific study. The communities that harbor the majority of candidate taxa on each island are as follows: Kaua'i and O'ahu -- mixed mesophytic forest (56% and 36.4%), low elevation rain forest (14.3% and 40%); Moloka'i and Lana'i -- dryland sclerophyll woodland (21% and 23%), mixed mesophytic forest (37% and 26%); Maui and Hawai'i

-- dryland sclerophyll woodland (16.7% and 13%), mixed mesophytic forest (26% and 20%), low elevation rain forest (16% and 25%), montane rain forest (11% and 10%), subalpine forest and scrub (5% and 10%).

Although the differences among islands and habitats is partly due to the history of man's impact on each island, it probably is more a reflection of an island's age, which affects its topography and the diversity within communities. Topography, in turn, relates to species distributions; that is, the older and more dissected an island, the more local are species distributions. The primary contributing factors to the degradation of native Hawaiian ecosystems are the elimination of habitat through agricultural uses, such as cattle ranching and sugar cane and pineapple cultivation; through urbanization; and through the activities of hoofed animals. Numerous alien plant species in genera such as Psidium, Lantana, Passiflora, and Pennisetum, which dominate habitats formerly occupied by native vegetation, are responsible for smothering existing native species and preventing their regeneration. A myriad of other problems contributes to the deterioration of the Hawaiian flora, including the loss or decline of pollinators, inbreeding depression, and introduced insects such as the black twig borer (Xylosandrus compactus).

Evaluation of the current status of the Hawaiian species of Amaranthaceae, Fabaceae, and Malvaceae clearly shows that members that occur in coastal areas, dryland sclerophyll scrub, and mixed mesophytic forest are currently vulnerable, endangered, or even presumed extinct. Moreover, since nearly all members of these families are in some state of decline, we might generalize that if other families were examined, we would find a similar situation. A chronicle of man's activities in the 'Ewa Plains area on O'ahu is reconstructed as an example of the rapid degradation of a natural community by man.

Public education is one of the principal requirements for initiating adequate conservation programs. There is also a critical need for an adequate classification and inventory of the flora. A project initiated in 1982 at the Bernice P. Bishop Museum to produce a Manual of the Flowering Plants of Hawai'i will provide a modern framework for further in-depth studies of Hawaiian plants. At the same time, it is essential to establish and maintain natural and semi-natural areas in as many community types as possible. Studies of population biology, ecology, and biosystematics are needed in order to develop effective management and conservation programs.

INTRODUCTION

The Hawaiian Archipelago is a great chain of 132 volcanic islands, seamounts, shoals, atolls, and reefs that stretches 2,451 km southeast to northwest across the Tropic of Cancer. The 8 main islands, Hawai'i, Maui, Kaho'olawe, Lana'i, Moloka'i, O'ahu, Kaua'i, and Ni'ihau, make up over 99% of the total land area of 16,641 km^2. The remaining 1%, less than 15 km^2, is comprised of small islets off the shores of the main islands and the Northwestern Hawaiian Islands (Armstrong 1973). The main islands range in age from about 400,000 years at Mauna Kea on the island of Hawai'i to 5 million years on Kaua'i and 3 million years on Ni'ihau. Midway Islands, near the northwestern end of the chain, are about 27 million years old (see summary in Olson and James 1982). If the Emperor Chain of seamounts, which extends northward to Meiji Guyot near the Aleutian trench, is also considered to have arisen over the Hawaiian hot spot (Morgan 1972; Dalrymple, Lanphere, and Jackson 1974), then land could have existed in the vicinity of the present main Hawaiian Islands for over 70 million years, which is the apparent age of Meiji Guyot (Scholl and Creager 1973).

The great diversity of climates in Hawai'i supports a wide range of vegetation types including coastal, dryland sclerophyll scrub and woodland, mixed mesophytic woodland and forest, subtropical rain forest and cloud forest, and xeric alpine scrub.

The Hawaiian Islands have long been known for their remarkable diversity of ecological environments and high level of endemism in their fauna and flora. The disharmonic nature of the flora is directly related to the extreme isolation of the islands; Hawai'i is in fact the most isolated major island group in the world. The native flora consists entirely of waif elements derived by long-distance dispersal. From approximately 270 flowering plants that successfully colonized the islands, evolution has led to roughly 1,200 species of flowering plants, about 95% of which occur only in Hawai'i (Fosberg 1948). Approximately 32 genera (several of questionable status) are endemic, and a few others, such as Charpentiera, have a limited distribution elsewhere, resulting in approximately 16% endemism at the generic level. Interestingly, about 22% of the flowering plant families of the world are found in Hawai'i and none are endemic.

Isolated islands are well known to be vulnerable to the influences of man, both directly through development and habitat destruction, and indirectly through animal and plant introductions (Carlquist 1974). This vulnerability results directly from the evolution of a native biota in the complete absence of man and grazing mammals. In Hawai'i, the introduction of feral animals has been extremely detrimental to the native flora. The decline or elimination of native plant populations is compounded by their often localized distributions and small population sizes.

About 1,600 years ago Polynesian explorers arrived on the pristine shores of these islands (Kirch 1982). They burned and cleared much of the lowlands for their crops and villages (Kirch 1982); pigs (Sus scrofa ssp.) and rats (Rattus exulans) were introduced (Kirch 1982); and some of the introduced plants, such as kukui (Aleurites moluccana), began to compete with the native ones for available space. Undoubtedly some native plant species became extinct, but there is no way of knowing how many. Destruction of native plants greatly increased with the introduction of goats (Capra hircus) and European pigs (Sus scrofa) by Captain James Cook in 1778. Fifteen years later another English sea captain, George Vancouver, brought sheep (Ovis aries) and cattle (Bos taurus). Goats and cattle probably have caused more destruction than any other creature save man in Hawai'i. A kapu (taboo) placed on the killing of cattle allowed the growth of enormous herds, until the destruction of native forests was so great that man was forced to contain or destroy the animals. Weedy plant species undoubtedly followed the animals, taking advantage of the disturbance they made.

In this paper we attempt to summarize, based on existing information, the status of the native flowering plants of the Hawaiian Archipelago. The relative endangerment of the Hawaiian flora is evaluated by comparing the numbers of candidate threatened and endangered taxa occurring on each island and in each major ecological zone. The data compiled by the U.S. Fish and Wildlife Service (1980) is derived from the most recent comprehensive list of endangered and threatened plants. Principal past and present threats to native habitats are reviewed for each island. Then the current status of the Hawaiian members of the families Amaranthaceae, Fabaceae, and Malvaceae are discussed to emphasize not only the wide extent to which our flora has deteriorated (especially in this century), but also to indicate the range of factors responsible for its degradation. Finally, the examination of a specific locality ('Ewa Plains) through time is made to obtain a perspective on the sequence and rate of destruction of native habitats in the Hawaiian Islands.

TAXONOMIC PROBLEMS

In order to assess the status of the native flowering plants of Hawai'i, we must first classify and inventory the taxa. A comparison of various estimates of the number of taxa in the Hawaiian flora shows a very wide difference of opinion. The great disparity in the estimates of the number of native Hawaiian plants and their delimitation has been due largely to differences in individual interpretation of observed variability and the paucity of population studies of Hawaiian plants. The extremes in number range from that presented in Hillebrand's flora (1888) which included 705 species, to estimates by St. John (1973), of 1,394 native species (with a fair number described since 1973) and even 20,000-30,000 species as suggested by Degener and Degener (1975). Work currently in progress at the Bishop Museum to produce a Manual of the Flowering Plants of Hawai'i suggests that there are roughly 1,200-1,300 native species. Most studies of Hawaiian plants have been descriptive and taxonomic in nature, based primarily upon the comparison of gross morphological characters of individual plants. Some Hawaiian botanists have maintained to the present day a tradition of describing most variations in plant species in a formal sense, resulting in very large numbers of species, varieties, and forms, many of which are clearly artificial. In order to perform meaningful scientific studies and formulate effective management practices for the remaining Hawaiian flora, we must first have classifications that enable information retrieval and formulation of general biological principles. Indeed, the soundness and utility of a classification can be tested by the ease with which it accommodates information derived from new characters as well as new populations or species.

Modern methods of delimiting species are firmly founded in comparative morphology but are applied in the context of populations and reproductive systems, not merely for cataloging differences between specimens. A great range of techniques and methods is currently employed by systematists in their investigations of the classification, reproduction, and evolution of flowering plants, including chemical analysis, cytology, genetics, hybridization, analysis of breeding systems, common garden experiments, and demographic studies. These techniques and methods also can be exceedingly useful in discerning evolutionary, genetic, and ecological principles that govern the dynamics of plant populations, as well as in formulating realistic management guidelines.

RARE AND ENDANGERED SPECIES OF HAWAIIAN FLOWERING PLANTS

Rare and Endangered Species of Hawaiian Vascular Plants by Fosberg and Herbst (1975) was the first published attempt to give a comprehensive summary of the status of our native vascular flora. This work formed the basis for the Hawaiian taxa included in the Smithsonian Institute's report to Congress published in 1975. It was accepted under the Endangered Species Act and was published by the U.S. Fish and Wildlife Service (1975) as a "Notice of Review." Subsequently, the Service (1976) published a proposal to list some 1,700 plants as endangered, of which 895 are native to Hawai'i. The latest complete revision by the Service was published on December 15, 1980 in the Federal Register.

In the 1980 summary, plants were grouped into 3 categories: 1) plants for which sufficient information exists to support listing the species as endangered or threatened (includes taxa which possibly are extinct); 2) species probably endangered or threatened, but for which more information or research is required to support listing; and 3) plants believed extinct (3A), those with taxonomic problems (3B), and those no longer thought to be endangered or threatened, based on new information (3C). In the 1980 list there are 793 candidate taxa from Hawai'i out of 2,560 candidates for the entire United States, representing 31% of the total taxa listed. California has nearly as many (30%) but has a flora with many times more species. No other state has anywhere near the magnitude of Hawai'i's problem. Although taxonomic review of the Hawaiian flora will reduce the number of taxa considered valid entities, roughly 50% of the vascular flora will still be considered candidate threatened and endangered plants. This problem is discussed further below. In fact, 177 native vascular plants (ca. 10% of the Hawaiian flora) are already known or thought to be extinct, whereas only 106 taxa (0.5%) are extinct from the entire continental United States, including Alaska. The numbers of presumed extinct plants in Hawai'i should be viewed with caution, however, since some Hawaiian species presumed extinct may still be extant. The principal reasons for this are: 1) most of these taxa may have very local and poorly understood distributions, making them very difficult to locate; or 2) many species are exceedingly difficult to identify unless examined during the brief periods when they are in flower and/or fruit. These problems are often compounded by the inaccessibility of many areas in the Islands, either because of the terrain or because scientists increasingly have difficulty obtaining access to private lands.

The fact that there are a large number of highly technical or artificial taxa currently recognized in Hawai'i creates a very serious problem in making an overall evaluation of threatened and endangered species for the Hawaiian Islands. When a contemporary taxonomic review of all the native Hawaiian plants is completed, it is fully expected that the actual number of native species recognized will fall to between 1,200 and 1,300, and we project that the number of taxa recognized on the current list of candidate threatened and endangered plants published by the U.S. Fish and Wildlife Service (1980) will be reduced by about 25-35%. A revised list thus would contain approximately 550-600 taxa, representing roughly half of the total flora using the revised total of 1,200-1,300 species. When we compare these figures to those obtained with the number of native taxa on the 1980 list and previous estimates of native species of 1,500-2,000, the result is a similar percentage of 42-56%. Therefore, it appears very unlikely that a contemporary taxonomic review and subsequent reduction in the numbers of plant species recognized in Hawai'i will have any effect on any overall conclusions drawn from existing lists to establish percentages of candidate taxa on each island and in each major plant community type.

Endangered Species Program

The Federal government presently has 11 Hawaiian plants listed as endangered, 1 has been proposed as endangered, and the documentation for an additional 9 is under review by the U.S. Fish and Wildlife Service's Washington office (table 1). Habitat modification for agricultural or urban development and foraging by introduced herbivores, both past and present, probably are the 2 greatest threats to our native flora.

All the species listed in table 1 are comprised of small, restricted populations. This, too, is a major threat to the continued existence of the plants, but only specific threats have been included in the table. Small numbers of individuals and a restricted distribution make a species particularly vulnerable to environmental disturbances, since a single action such as a fire or natural fluctuation in the population could eliminate the taxon. The presence of small populations also leads to inbreeding, which may result in a loss of reproductive vigor and evolutionary potential due to the concomitant reduction of genetic recombination in normally outcrossing or dioecious species.

Distribution of Threatened and Endangered Plants

Are there discernible patterns to the distribution of threatened and endangered plants in the Hawaiian Islands? Do plants occur in specific habitats or on specific islands? What are the proportions on each island? In order to begin to answer such questions, we examined, by island and ecological zone, the distribution of each taxon included in the 1980 list. The ecological distribution of each taxon was based on a subjective analysis of known collection sites in the plant

Table 1. Native Hawaiian plants listed as endangered (L), proposed to be listed (P), or candidates under review by the Washington office, U.S. Fish and Wildlife Service (C). Data on threats from U.S. Fish and Wildlife Service.

Taxon	Distribution by Island[1]	Status	Threats
Abutilon menziesii	H,L	C	Herbivory by axis deer, cattle, goats, Chinese rose beetle (*Adoretus sinicus*); conversion of habitat for agricultural purposes; fire potential (Funk and Smith 1982).
Achyranthes splendens var. *rotundata*	O	C	Modification of habitat, in the past for agricultural purposes, at present with the development of the harbor, parks and industrial complex at Barber's Point; competition by alien species (Nagata 1981)
Argyroxiphium sandwicense var. *sandwicense*	H	C	Browsing by alien feral mouflon sheep damages the plants and, secondarily, its habitat; adverse management practices as removal of unnecessarily large quantities of fruit for propagation purposes; present exclosure ineffective against sheep (Carr 1981b).
Bidens cuneata	O	L	Soil compaction; erosion promotion; trampling due to hikers; alien species competition; overcollection (Herbst and Takeuchi 1982; Herbst 1984).
Chamaesyce skottsbergii var. *kalaeloana*	O	L	Construction of Barber's Point deep draft harbor; competition with alien vegetation (Fay 1980, 1982).

Taxon	Distribution by Island	Status	Threats
Cyanea superba	O	C	Habitat disturbance by feral cattle, goats, and pigs; invasion of habitat by aggressive alien plants; fire potential from Makua Valley military hikers, hunters, or from impact area (Obata and Smith 1981).
Gardenia brighamii	O, Mo, L, M, H	P	Fire; grazing by introduced herbivores; habitat modification in early and recent times for agricultural purposes; invasion of habitat by alien plants; fruit and seeds eaten by rodents; damage by black twig borer and other alien insects (Gagne 1982).
Gouania hillebrandii	M	L	Browsing, grazing, trampling by feral and domestic livestock; removal of native vegetation with its replacement by alien species; predation by the hibiscus snow scale Pinnaspis strachani (Herbst 1983a).
Haplostachys haplostacha var. angustifolia	H	L	Invasion of fountain grass and other alien species; fire; browsing by feral goats and sheep; military training operations (Herbst and Fay 1979).
Hibiscadelphus distans	K	C	Browsing by feral goats; vandalism or accidental damage from hikers and hunters; fire and damage by rats and the Chinese rose beetle are potential threats (Herbst 1978).

Table 1. Continued.

Taxon	Distribution by Island	Status	Threats
Kokia cookei	Mo	L	Extinct in the wild, 4 grafted plants at Waimea Arboretum, one sapling at Kew (Fay 1979).
Kokia drynarioides	H	L	Grazing and habitat modification by livestock and browsing of plants; invasion and modification of habitat by fountain grass; range fire; destruction of seeds by rodents (Herbst 1983b).
Lipochaeta venosa	H	L	Threats same as Haplostachys (Herbst and Fay 1979).
Mezoneuron kavaiense	K, O, M, H	C	Grazing and browsing by domestic and feral animals; habitat modification by introduce plants; seeds eaten/destroyed by rodents; damage by alien insects as the black twig borer; harvesting of wood (Lamoureux 1982)
Panicum carteri	O	L	Pedestrian traffic; potential vandalism; fire; habitat modification (Herbst and Fay 1981, 1983).
Remya mauiensis	M	C	Browsing, grazing, trampling by feral and domestic animals; now fenced by State (Herbst 1979).
Santalum freycinetianum var. lanaiense	L, M	C	Modification of habitat by domestic and feral animals; conversion of habitat to agricultural land; introduction of alien

Taxon	Distribution by Island	Status	Threats
			plant species; fruit predation by rats (Carr 1981a).
Scaevola coriacea	L, M, O, K, Mo, Ni, H	C	Conversion of habitat into pastures and cane fields, housing and commercial tracts, recreational parks and golf courses; use of Mokuho`onihi Islet as a bombing site (Carr 1981c).
Schiedea adamantis	O	L	Fire potential; overcollection; hikers; alien species invasion and competition (Herbst and Takeuchi 1982; Herbst 1984).
Stenogyne angustifolia var. angustifolia	H	L	Threats same as Haplostachys (Herbst and Fay 1979).
Vicia menziesii	H	L	Cattle; logging; reforestation project; pigs; rodents eat seeds and cut stems (McManus, Altevogt, and MacBryde 1978).

[1] H = Hawai`i; K = Kaua`i; L = Lana`i; M = Maui; Mo = Moloka`i; N = Ni`ihau; O = O`ahu.

community classification scheme presented in table 2. If a particular taxon occurred in more than one plant community, it was counted in each category; thus the total number of taxon occurrences in the table is somewhat higher than the number of taxa evaluated. The results of this evaluation are summarized in table 3, which includes only the flowering plant taxa. The data clearly show that candidate threatened and endangered plants have definite distribution patterns both by island and habitat type. O'ahu has the highest percentage (27.3%) of candidate rare taxa, followed by the islands of Hawai'i (18.3%), Maui (16.8%), and Kaua'i (14.0%). Ni'ihau (1.5%) and Kaho'olawe (0.7%) have low numbers not only because of the low habitat diversity of these islands compared to others, but also because the native biota already largely was gone by the time these islands were first studied. The data also show, as is well known, that in Hawai'i the ecological zones most severely degraded are mixed mesophytic forest (C), which harbors nearly one-third of the total candidate taxa, and low elevation rain forest (D1), with nearly 24% of the total. Not indicated by this analysis was the severe, early degradation of coastal (with 9.5%) and lowland (with 14.7%) vegetation that occurred prior to their scientific study. Moreover, the percentage of endemism of coastal plants is much less than in other ecosystems and thus a coastal plant usually would not appear in a threatened and endangered species list unless threatened throughout its entire range.

Let us now discuss on an island-by-island basis the patterns of distribution of candidate threatened and endangered plants (including those presumed extinct) and the past and current threats to native vegetation on each.

Ni'ihau. This island has been poorly studied. The principal early collections from Ni'ihau were made by Lay and Collie, 1826-27; Remy, 1851-55; and Brigham, 1865 (Forbes 1913). Most of the native vegetation was destroyed by cattle, sheep, and goats prior to the collections made by St. John in 1947 and 1949 (St. John 1959, 1982), when the remaining native vegetation was restricted to cliffs, perched rocks, and a small fenced area around a spring (H. St. John, pers. comm.). At one time Ni'ihau probably had coastal, dryland sclerophyll forest, and based on single collections of *Cheirodendron trigynum* and *Delissea undulata*, some elements of mixed mesophytic forest. Since the latter type of habitat is the most species-rich in Hawai'i, the total number of species listed in table 3 for Ni'ihau most likely is not representative of the diversity of the original flora nor of the number of extinctions that have occurred.

Table 2. Overview of ecological zonation scheme for the high Hawaiian Islands* (letter symbols adapted to Ripperton and Hosaka 1942 map).

I. Zonal Ecosystems [controlled primarily through macroclimate]

1. Xerotropical (leeward lowland to submontane)

A. Savannah and dry grassland [Prosopis savannah and Heteropogon-Rhynchelytrum grassland]

B. Dryland sclerophyll forest (or scrub) [Metrosideros-Diospyros open forests; replacement vegetation: Leucaena scrub and forest]

C. Mixed mesophytic forest (woodland or scrub). [Open Acacia forests; replacement vegetation Psidium guajava, Eugenia cumini forests or woodland]

2. Pluviotropical (windward lowland to upper montane)

D1. Lowland rain forest [Metrosideros forests]

D2. Montane rain forest [Metrosideros-Cibotium and dominantly Cibotium forests]

D3. Upper montane rain or cloud forest [Cheirodendron or Acacia-Metrosideros mixed forests]

3. Cool tropical [upper montane to alpine; only on Maui and Hawai'i]

E1. Mountain parkland and savannah [Acacia-Sophora tree communities, Deschampsia tussock grassland]

E2. Subalpine forest and scrub [Sophora-Myoporum tree communities, Styphelia-Vaccinium-Dodonaea-Metrosideros scrub communities]

E3. Sparse alpine scrub [Styphelia, Vaccinium] and moss desert [Rhacomitrium lanuginosum var. pruinosum]

Table 2. Continued.

II. Azonal Ecosystems [controlled primarily through edaphic factors]

4. Coastline
   - windward beach, dune and rock-substrates [Scaevola scrub, Pandanus and Hibiscus tiliaceus forests]
   - leeward beach, dune and rock-substrates [Prosopis scrub and woodland]

5. Bogs
   - low- and mid-elevation bogs
   - montane bogs

6. Geologically recent
   - vegetation on new volcanic materials [e.g., Metrosideros-Sadleria, Gleichenia, and Lycopodium]
   - lava tubes and other recent geological features

7. Aquatic
   - fresh water lakes
   - streams
   - coastal brackish and marine ponds

8. Cliffs

* Synthesized by Gagne and Mueller-Dombois (n.d.) from earlier works (Egler 1939; Ripperton and Hosaka 1942; Krajina 1963, Knapp 1965; Mueller-Dombois and Krajina 1968; Fosberg 1972).

Table 3. Occurrence by island and ecological zone of the flowering plant taxa listed in the December 15, 1980 Federal Register. Ecological zone symbols are those listed in Table 2.*

	Ecological Zone															
	4	A	B	C	D1	D2	D3	E1	E2	E3	5	6	8	?	Total	%
Main Islands (HI):																
Ni`ihau (Ni)	3	5	3	1	--	--	--	--	--	--	--	--	2	2	16	1.5
Kaua`i (K)	6	0	12	87	22	1	9	--	--	--	8	--	4	5	154	14.0
O`ahu (O)	23	0	17	109	120	4	11	--	--	--	1	--	3	11	299	27.3
Moloka`i (Mo)	13	0	23	39	13	11	1	--	--	--	0	--	1	4	105	9.6
Lana`i (L)	9	3	24	28	27	2	9	--	--	--	--	--	0	4	106	9.6
Maui (M)	14	3	31	48	30	20	5	1	10	6	2	1	1	13	185	16.8
Kaho`olawe (Ka)	1	1	6	--	--	--	--	--	--	--	--	--	0	0	8	0.7
Hawai`i (H)	14	3	26	41	50	20	7	4	20	2	2	0	0	12	201	18.3
Offshore Islands:																
Mokoli`a	1	--	--	--	--	--	--	--	--	--	--	--	--	--	1	0.1
Ka`ula	1	--	--	--	--	--	--	--	--	--	--	--	--	--	1	0.1

Table 3. Continued.

	Ecological Zone													?	Total	%
	4	A	B	C	D1	D2	D3	E1	E2	E3	5	6	8			
Northwestern Hawaiian Islands (NWI):																
Kure (Ku)	5	--	--	--	--	--	--	--	--	--	--	--	--	--	5	0.4
Midway (Mi)	3	--	--	--	--	--	--	--	--	--	--	--	--	--	3	0.3
Pearl & Hermes (PH)	1	--	--	--	--	--	--	--	--	--	--	--	--	--	1	0.1
Lisianski (Li)	1	--	--	--	--	--	--	--	--	--	--	--	--	--	1	0.1
Laysan (La)	7	--	--	--	--	--	--	--	--	--	--	--	--	--	7	0.6
Necker (Ne)	1	--	--	--	--	--	--	--	--	--	--	--	--	--	1	0.1
Nihoa (N)	1	--	4	--	--	--	--	--	--	--	--	--	--	--	5	0.4
Total	104	15	146	353	262	58	42	5	30	8	13	1	11	51	1099	
%	9.5	1.4	13.3	32.1	23.8	5.3	3.8	0.5	2.7	0.7	1.2	0.1	1.0	4.6		

* The question mark (?) on the habitat type axis indicates that habitat is unknown; hyphens (--) indicate that a particular community type does not occur on that island.

Kaua'i. More than one half (56%) of the candidate threatened and endangered species on Kaua'i occur in the mixed mesophytic forest of the Koke'e region. Currently, this entire area is very vulnerable, largely due to present land management practices. The area has been developed for agricultural uses such as grazing cattle and also has been impacted by the development of water collecting systems for sugar cane fields at lower elevations. Another major threat to the native plants is competition with alien plant species such as the blackberry (Rubus argutus, incl. R. penetrans), introduced for its fruit; the faya tree (Myrica faya), for reforestation (Neal 1965); the banana poka (Passiflora mollissima), as an ornamental; and the karakanut (Corynocarpus laevigata) which was broadcast by air over the Koke'e area after World War I. Development for recreation also has had a very great impact on the area through extensive hiking trails; construction of vacation cabins; the deliberate introduction of animals such as horses for riding, and the black-tailed deer (Odocoileus hemionus) and Guinea fowl (Numida meleagris) for hunting; as well as the maintenance of populations of feral goats and pigs for hunting.

Mixed mesophytic and rain forest ecosystems on Kaua'i are still not fully known and have not been recently studied. The rediscovery of species presumed extinct, such as 2 populations of Remya kauaiensis and new populations of Isodendrion forbesii (T. Flynn, pers. comm.), indicates that our knowledge of Kaua'i is yet incomplete.

Kaua'i has the highest number of candidate threatened and endangered bog species (8) for Hawai'i, primarily due to the fact that it has the most extensive bog system in the Islands. Since most alien plant species are not adapted to bog environments, bogs are among the least disturbed habitats in the Islands. In bogs alien species are principally confined to hiking trails and their immediate vicinity. Other than hiking trails the only significant disturbance to the bogs appears to be from invasion by pigs, but this can be a considerable disruptive factor as seen in parts of the Alaka'i Swamp (W. Takeuchi, pers. comm.).

O'ahu. Like Kaua'i, this older island is highly dissected; as a result, ecological zones in mountainous areas often have abrupt transitions and therefore species often have very localized distributions. Nearly 75% of the total candidate threatened and endangered plant taxa on O'ahu occur in mixed mesophytic forest and low elevation rain forest, the predominant montane communities on O'ahu. Nearly 30% of the total candidate taxa on O'ahu (70% of the low elevation rain forest category) are in the genus Cyrtandra. The large number of Cyrtandra species (83) is partly the result of a detailed study of the O'ahu species by St. John (1966) and the description of a large number of artificial taxa, including species based on minor morphological features and species known from single specimens which now appear to represent hybrids. Despite these problems, a large number of Cyrtandra species on O'ahu resulted from the isolation of Cyrtandra populations in many dissected valleys. Wind direction is the same as the long axes of the valleys, so the spread of plants with low dispersibility such as Cyrtandra is primarily up and down the valleys. Moreover, the narrow ecological range of most Cyrtandra species (mixed mesophytic forest to low elevation rain forest) further limits dispersal into adjacent valleys. Careful evaluation of Cyrtandra on O'ahu is needed after a more conservative taxonomy is established and possible hybrids are removed from consideration. On other islands the situation for speciation is different. Either they are geologically too young to have developed such intricate valley and gulch topography with low elevation rain forest (East Maui and Hawai'i), or they are too highly eroded (Kaua'i).

The remaining 37 candidate threatened and endangered taxa of low elevation rain forest of O'ahu (30% of O'ahu rain forest category) occur primarily in the Ko'olau Mountains, where the situation is among the most critical in the Islands; the list of threats here is almost endless. Degradation of habitats in the Ko'olau Mountains began with the development of trails by early Hawaiians that presumably allowed movement of naturalized species up into the range. Low elevation areas were altered even more by prehistoric Hawaiians through cultivation of taro and sweet potatoes in many valleys such as Manoa and Nu'uanu (C. Lamoureux, pers. comm.). Impacts in this area have been far greater since the arrival of western man. Severe damage has resulted from urbanization, cattle, fires, military use, and introduction of alien plant species. The grazing of cattle probably has been the most detrimental to the native biota; for example, the remaining forests of the lower slopes of Manoa Valley were essentially denuded by cattle and woodcutters during the earlier parts of this century (Campbell 1920). Areas such as Manoa are now reforested entirely with introduced species such as Psidium cattleianum, Eucalyptus spp., Eugenia spp., and Persea americana. More recently, the military has leased large areas of the Ko'olau Mountains for training, resulting in many plants being trampled in military exercises and destroyed in fires from the explosion of ordnance. Fires also have altered many areas of native vegetation that are not especially fire resistant and subsequently have encouraged invasion by alien species (Smith, this volume).

Introduced plants now constitute the bulk of the vegetation below 600 m elevation. In addition to the alien plants mentioned above, other species such as Koster's curse (Clidemia hirta) have severely impacted the rain forest vegetation of the Ko'olau Mountains since introduction prior to 1941 (Wester and Wood 1977). Clidemia has since colonized the Wai'anae Mountains, where it probably will have the same impact. Other plants such as Citharexylum caudatum, which currently is spreading into the Ko'olau Mountains out of Manoa Valley, may repeat the pattern exhibited by Clidemia. In summary, almost no undisturbed native plant communities occur below 600 m elevation other than a few scattered patches of native coastal strand vegetation. Only a few hardy native species such as Canthium odoratum and Alyxia olivaeformis still occur in small patches mixed in the forests and scrub vegetation consisting of alien species.

Approximately 36% of the O'ahu taxa listed in the 1980 list occurs in mixed mesophytic vegetation. The extant species in this category occur primarily in the Wai'anae Mountains, the oldest on O'ahu, where a very diverse mixed mesophytic forest and perhaps the best development of this type in the Islands occurs. Mixed mesophytic vegetation formerly also was in areas above Honolulu where much early collecting was done; however, the forest now has been nearly eliminated there. There are many threats to the unique vegetation of the Wai'anae Mountains, including the construction of military installations such as radar tracking stations and Nike missile sites, feral animals, and introduced plants such as guava (Psidium spp.) and koa haole (Leucaena leucocephala).

The low elevation and coastal zones of O'ahu have fared even worse than the uplands. Most coastal and dryland sclerophyll vegetation has been completely eliminated by land development.

Moloka'i and Lana'i. The distribution and total number of candidate threatened and endangered taxa are very similar for these 2 islands. Most of the lower elevation vegetation on both islands has been largely replaced by grazing land and pineapple fields. Feral animals also have played a major role in the degradation of the native ecosystems. Forestry plantings of alien tree species such as Eucalyptus spp., paper bark (Melaleuca quinquenervia), Alnus spp., and Pinus spp. for erosion control at higher elevations have prevented the return of native rain forest species to many areas of East Moloka'i. A few pristine and nearly inaccessible areas such as Oloku'i Plateau still exist on Moloka'i. The Nature Conservency recently purchased conservation rights to a portion of the remaining native rain forest on East Moloka'i and created the Kamakou Preserve. It presently is developing a management system that includes removal of alien vegetation and exclusion of feral animals from the preserve (Holt and Fox, this volume).

In the lowlands of Lana'i almost all native ecosystems have been eliminated and only small pockets of native vegetation still remain, such as at Kanepu'u. A few native plants such as Lipochaeta heterophylla, Gossypium sandvicense, Erythrina sandwicensis, and Chamaesyce celastroides persist in these areas.

Roughly 62% of the Lana'i taxa in table 3 are restricted to the Lana'ihale area, which harbors the only mixed mesophytic and rain forest on the Island. Lana'ihale formerly was degraded by feral goats, which were essentially eliminated in the 1930's. More recently, as the goat population increased, they were again reduced significantly. Another important impact to Lana'ihale has been caused by the planting of alien species along the crest. Good remnants of native vegetation still exist in the deep gulches of this area; however, a continuing major threat is the presence of axis deer (Axis axis).

Maui and Hawai'i. The distribution and total number of threatened and endangered plants on these 2 islands are very similar but differ from the other islands. Apparently fewer endangered species occur on Maui and Hawai'i in each habitat. The age, elevation, and geological structure of each island govern the types of habitats that develop, which in turn influences floristic diversity. The younger islands of Maui and Hawai'i are topographically less dissected and thus the transitions from habitat to habitat are generally more gradual. Therefore, specific plant community types and species distributions are often wider and more continuous on the younger islands. In contrast, topography of the older islands of Kaua'i and O'ahu is more varied and highly dissected, resulting in more opportunities for speciation as well as narrower species distributions.

Mountains on Maui and Hawai'i are high enough to extend above the inversion layer and thus have 3 ecological zones not present on the older, lower islands: mountain parkland, subalpine forest, and alpine scrub (table 2). These islands also have the largest areas of montane rain forest. Although the factors mentioned above may partially explain the numbers of threatened and endangered species and their distribution (table

3), another factor may be our lack of knowledge of Maui and Hawai'i. Both islands had large areas altered by cattle and other agricultural practices long before their floras were extensively studied (Stone, this volume). Therefore, it seems likely that some plant species were extinct before they could be discovered and described (St. John 1976, 1978). Extinctions have been well documented for birds at least on Kaua'i, O'ahu, and Moloka'i (Olson and James 1982). They found that the fossil avifauna consists of between 2 and 3 times as many species as that known historically.

As a direct result of man's use of the land, there are candidate threatened and endangered plants in nearly every habitat type on these 2 islands. Some examples of man's impact are discussed below.

1. Agriculture. Prehistoric Hawaiians cleared and intensively cultivated large tracts of land in the Waimea area on the island of Hawai'i (Clark and Kirch 1983). Cattle were introduced in the 1790's and protected by a kapu (taboo). This resulted in large herds of feral cattle and led to the establishment of large ranches such as Parker Ranch, among the largest privately owned ranches in the United States. On Maui several large ranches cover extensive areas of Haleakala. Sheep ranches such as the one at Humu'ula, Hawai'i, also were established on these islands, but none are still in operation.

Crop cultivation also has irreversibly changed some areas. Hawaiians cleared extensive lowland areas prior to Cook's arrival. Beginning in the middle 1800's, large tracts of land were cleared on Maui for wheat, Irish potatoes, pineapple, and vegetable crops. Small vegetable and flower truck farms still exist, including those of Kula, Maui, and Waimea (Kamuela), Hawai'i. Sugar cane and more recently macadamia nut trees occupy extensive acreage on both islands. The largest known population of *Neowawraea phyllanthoides* (formerly, *Drypetes*), an endemic species which is nearly extinct, was greatly reduced when new land was cleared for a macadamia nut farm on the Kapu'a tract, Hawai'i.

2. Silviculture. Although logging in the past has been a relatively minor industry in Hawai'i, silviculture has already had a major impact on the native vegetation, and it may be important in the future if native trees are used for energy production. Native species, primarily koa (*Acacia koa*), are harvested, and plantations of eucalyptus and other aliens have frequently been established by replacing the native vegetation. In the past, tree ferns (*Cibotium* spp.) have been harvested for their starch, and the scales on the

fronds were used for stuffing mattresses and furniture. Currently, croziers are still harvested as a vegetable, and the trunks are used as a growth medium in the large orchid industry and whole plants in landscaping.

3. Introduced species. Fountain grass (Pennisetum setaceum) is a good example of an alien weed that has had a great impact on the environment on the island of Hawai'i. Originally introduced as an ornamental in the early 1920's on the Hu'ehu'e Ranch, fountain grass is an aggressive invader and now is becoming widespread and abundant primarily in dry areas. This species creates a fire hazard by adding large amounts of organic matter to the ecosystem. Moreover, it is a fire climax species and among the first pioneers to quickly move into an area after a fire. This appears to prevent other plants from becoming established (Smith, this volume).

Openings or disturbances of an area, as from the browsing and grazing of feral animals, activities by man, or a phenomenon like 'ohi'a (Metrosideros polymorpha) dieback (Mueller-Dombois, this volume), allows the entry of alien species into native communities. In addition to directly destroying native plants, feral animals also spread introduced plants. For example, it is probable that introduced game birds recently have spread the European olive (Olea europea) near Waimea on the island of Hawai'i. Passiflora mollissima and Myrica faya have been spread by feral pigs and game birds in Hawai'i Volcanoes National Park and other areas (Warshauer et al. 1983; L. Stemmermann, pers. comm.).

4. Development. Urbanization has occurred rapidly in areas such as Kihei and Ka'anapali, Maui, and Waimea, Hawai'i. The principal impact of urbanization in these areas has not been the direct destruction of native communities, since most of the development is in already severely disturbed areas (primarily from sugar cane agriculture); rather, the effects have resulted indirectly from the continued demand on an area's resources, such as for the disposal of wastes and from the loss of natural water percolation.

Kaho'olawe. The current low number of candidate threatened and endangered taxa on Kaho'olawe may be due to our lack of knowledge of the original vegetation. Collections by Jules Remy sometime between 1851 and 1855, as well as studies of charcoal from archaeological excavations (G. Murakami, pers. comm.), give some indication that there once was coastal and dryland sclerophyll forest on Kaho'olawe. The discovery of charcoals of species never otherwise recorded from the

Island indicates that the prehistoric Hawaiians may have cleared much of the existing vegetation (G. Murakami, pers. comm.). Soon after their introduction, cattle, goats, and sheep largely eliminated the remaining native vegetation. Goats, however, continue to roam the island in large numbers and presumably prevent the return of any significant amount of native vegetation.

Northwestern Hawaiian Islands. With the exception of Laysan (Schauinsland 1899; Lamoureux 1963), the flora of these islands was not extensively studied prior to heavy human impact. Human use includes military operations (principally on Kure, Midway Islands, and French Frigate Shoals), guano mining and feather harvesting (Lisianski and Laysan), pearl oyster harvesting (Pearl and Hermes Reef), and introduction of rabbits probably for food (Lisianski and Laysan). In addition, archaeological evidence from Necker and Nihoa indicates that these islands were used by prehistoric Hawaiians.

With the exception of Nihoa, the flora is essentially coastal, consisting primarily of widespread strand species. There are 13 presently recognized taxa endemic to the Northwestern Hawaiian Islands. Among these, 4 are presumed extinct, *Achyranthes atollensis*, *Cenchrus laysanensis*, *Phyllostegia variabilis*, and *Pritchardia* sp. (undescribed from Laysan); the remainder are considered endangered or threatened.

STATUS OF HAWAIIAN AMARANTHACEAE, FABACEAE, AND MALVACEAE

In this section we examine the current status of native Hawaiian species of Amaranthaceae, Fabaceae, and Malvaceae. These families were arbitrarily selected as representative of the flora because we thought it would be useful to survey the status of several taxonomic groups in their entirety. In view of the space and time limitation only families that are small to medium-sized in Hawai'i were selected. Moreover, we selected families that occur predominantly in dryland sclerophyll to mixed mesophytic forest because it was clearly demonstrated in the previous section that these communities have been the most severely degraded so far in Hawai'i. Other examples of plants occurring primarily in rain forest will be given in the discussion. The analysis of the status and principal causes for the decline of the species in these families (table 4) is based primarily on observations by the authors and other Hawaiian biologists.

This summary clearly shows that most species in these families that occur in coastal, dryland sclerophyll scrub or forest and mixed mesophytic forest are

Table 4. Status and some causes of the decline of species in Amaranthaceae, Fabaceae, and Malvaceae in the Hawaiian Islands. Island symbols for distributions are those given in table 3

Taxon	Distribution by Island	Status[1]	Possible Reasons for Degradation
AMARANTHACEAE			
Achyranthes (3 spp.)	dryland scrub and coastal		
A. atollensis	NWI	Ex	Reasons for decline unknown.
A. mutica	K, H?	Ex	Probably severely impacted in pre-Cook times; known only from two collections.
A. splendens	O, M, Mo, L	V	Some populations appear stable, others severely depleted or lost by development.
Amaranthus brownii	N, dryland scrub	E	Perhaps below critical population size, gene pool severely reduced; low germination; perhaps may have been impacted in pre-historic times.
Charpentiera (5 spp.)	HI, mixed mesophytic forest	V	The black twig borer has severely reduced the numbers of plants of this genus (Hara & Beardsley 1979). A native insect in the endemic genus Mapsidius with no close relatives also affects the growing tips; it is unclear whether this is part of a natural cycle or the result of an

Taxon	Distribution by Island	Status	Possible Reasons for Degradation
			ecological imbalance (F. Howarth, pers. comm.).
Nototrichium (2 spp.)	dryland scrub		
N. humile	O	V	Very local species, could easily become extinct from habitat loss and competition with weeds.
N. sandwicense	HI	V	Decline due to habitat destruction.
FABACEAE			
Acacia (2 spp.)			
A. koa	HI, dryland to rain and subalpine forest	S	Currently widespread; however, fast-growing aliens such as Passiflora mollissima probably are outcompeting seedlings in certain localities and decreasing fecundity of adults. It was severely depleted in the past when land was converted to pastures. Introduced insects are also a periodic problem, e.g., Uresiphita polygonalis which defoliates plants, and the black twig borer (Hara & Beardsley 1979). Other threats include logging and increased infestation by koa rusts, Uromyces spp., now vectored by the alien insect Psylla uncatoides (Leeper & Beardsley 1973; Howarth, this volume), and

Table 4. Continued.

Taxon	Distribution by Island	Status	Possible Reasons for Degradation
			seed predation by such insects as the koa haole seed weevil, Araecerus levipennis (Stein 1983a, 1983b).
A. koaia	Mo, M, H, dryland forest	E	Severely depleted due to habitat degradation from feral and domestic animals, competition with introduced grasses, and fires. Also, it was popular with Hawaiians for making spears and canoe paddles (Rock 1913).
Canavalia (ca. 10 spp.)	HI, coastal to mixed mesophytic forest	S	Most of the species of this genus appear to be relatively stable. Canavalia kauensis, only recently described, first appeared in an experimental exclosure on Hawai`i, clearly indicating past degradation primarily by goats (Mueller-Dombois and Spatz 1972).
Cassia gaudichaudii	HI, dryland forest	V	Uncommon at the present time, primarily due to dryland forest destruction.
Erythrina sandwicensis	HI, coastal and dryland forest	S	Previously more widespread; possibly being replaced by Prosopis pallida or Leucaena leucocephala in parts of its range. Original bird pollinator presumed to be rare or extinct, but it currently is pollinated extensively by the Japanese white eye (D. Neill, pers. comm.).

Taxon	Distribution by Island	Status	Possible Reasons for Degradation
Mezoneuron kavaiense	HI, dryland to mixed mesophytic forest	R	Current low numbers are primarily due to conversion of much dryland and mixed mesophytic forest habitat to pasture and agricultural land, browsing by feral and domestic animals, rodents that eat its seeds, black twig borer infesting young wood, and fires. Perhaps depleted by previous use by Hawaiians for spears and in fishing (Rock 1913). It is currently under review by U.S. Fish & Wildlife Service for listing.
Sesbania (ca. 8 spp.)	HI, coastal and dryland forest	E or S	All species have been drastically impacted. Their habitat, low dry coastal areas, has deteriorated due to development of resorts, browsing by feral animals, and off-road vehicle traffic. The only populations which appear stable are those on Nihoa and Necker.
Sophora chrysophylla	HI, dryland to rain forest and subalpine forest	V	The single native species in this genus is common, but much less so than in the past, especially in subalpine scrub of Haleakala and Mauna Kea. In these areas its decline has primarily been caused by browsing of goats and sheep (Scowcroft 1983; Scowcroft and Sakai 1983) and specifically from the destruction of seedlings, thus preventing

Table 4. Continued.

Taxon	Distribution by Island	Status	Possible Reasons for Degradation
			regeneration (Scowcroft and Giffin 1983). With the eventual removal of sheep and feral goats from Mauna Kea, this population may be improving (Scowcroft 1983).
<u>Strongylodon</u> <u>ruber</u>	K, O, Mo, M, H, mixed mesophytic forest	?	This genus serves as an example of a group for which very little is known at present; thus we are unable to evaluate its current status.
<u>Vicia</u> <u>menziesii</u>	H, montane rain forest	E	It is an extremely rare species that is listed as endangered by the Endangered Species Act but currently is threatened by ungulates, rodents, and by bulldozing, logging, and conversion of its habitat to pasture (Warshauer and Jacobi 1982; Ralph, Pearson, and Phillips 1980). An estimate of 1,500-2,000 individuals was made prior to 1981. A recent survey by the State Division of Forestry and Wildlife showed a serious decline in the populations. Its taxonomic relationships were reviewed by Lassetter and Gunn (1979).
<u>Vigna</u> (3 spp.)			
<u>V. marina</u>	HI, coastal	S	An indigenous, widespread, successful strand plant. The Hawaiian populations currently are stable.

Taxon	Distribution by Island	Status	Possible Reasons for Degradation
V. o-wahuensis	K, O, Mo, coastal (to dryland scrub?)	R	Extremely rare; its severe decline is due to habitat loss: most of former habitat is now pasture, resorts, or beach parks.
V. sandwicensis	L, M, H, coastal	R	Same problem as V. o-wahuensis.
MALVACEAE			
Abutilon (4 spp.)			
A. eremitopetalum	L, dryland scrub	Ex	Extinction due to habitat destruction.
A. incanum	HI, coastal to dryland scrub	S	Apparently stable or only slowly declining.
A. menziesii	L, H, dryland scrub	E	Decline due to habitat destruction; presently only a few individuals known.
A. sandwicense	O, mixed mesophytic forest	R	Reasons for decline unknown. Seedlings have not been observed recently, perhaps due to rodent predation.
Gossypium sandvicense	HI, coastal	S	Situation of relative stability may rapidly change as coastal areas are developed.
Hibiscadelphus (6 spp.)	K, L, M, H, dryland to mixed mesophytic forest	E & Ex	Relictual at time of first collection in 1868; habitat destruction and rodents feeding on any seeds produced and

Table 4. Continued.

Taxon	Distribution by Island	Status	Possible Reasons for Degradation
			stripping the bark of stems perhaps will lead to extinction of entire genus relatively soon. Also, its unknown bird pollinator is probably rare or extinct. Presently 14 individuals are known collectively of *H. distans*, *H. hualalaiensis*, and *H. crucibracteatus* (Hobdy 1984), while *H. bombycinus*, *H. giffardianus* (2 wild seedlings in cultivation), and *H. wilderanus* are extinct.
Hibiscus (ca. 10 spp.)	HI, coastal to rain forest	S	Populations have been degraded in past; presently most species appear rather stable, with a few exceptions.
H. brackenridgei	O, Mo, L, M, H, dryland scrub	E	Extremely endangered due to habitat destruction and grazing by cattle.
Kokia (4 spp.)	K, O, Mo, H, mixed mesophytic to dryland forest	E or Ex	Situation very much like *Hibiscadelphus*; *K. cookei* (in cultivation) and *K. lanceolata* are extinct while *K. drynarioides* and *K. kauaiensis* are known from only small relictual populations. Principal causes for depletion are habitat destruction, stripping of bark and leaves by cattle, sheep, goats, and perhaps by previous use by Hawaiians to dye fishing nets (Rock 1913), and rodents destroying seeds.

Taxon	Distribution by Island	Status	Possible Reasons for Degradation
Sida (ca. 1Ø spp.)	HI, coastal to mixed mesophytic forest	S	Currently rather stable since this group grows fairly well in disturbed habitats, although it probably was more common in pre-contact times.

[1] The symbols in the status category, Extinct (Ex), Endangered (E), Vulnerable (V), and Rare (R), are adapted from IUCN Plant Red Data Book categories (Lucas and Synge 1977) and elaborated by Synge (1981, Appendix 3) except Stable (S), which is used for species that are known to be reproducing and apparently have relatively stable numbers.

currently vulnerable, endangered, or even presumed extinct. Moreover, most of the taxa classified as presently "stable" appear to have been more common in the past, but at the present time are either declining rather slowly or in some cases appear to be maintaining their present status. Other species, such as Vigna marina, which is an indigenous widespread strand plant, seems able to persist in severely altered habitats. Since nearly all members of these families are in some state of decline, we might generalize that if other families were examined, we would find a similar situation. It is possible that if the current threats are not removed, a great majority of the native Hawaiian ecosystems will be forever altered or destroyed in the next few decades. A great number of native species, however, appear to be able to persist in the face of extreme alteration of their habitat. For example, so far, with a hundred years of disturbance, about 10% of the known native species have become extinct. Fifty percent of the known extant species are candidates for threatened or endangered species classification. It is inevitable that if the native ecosystems continue to deteriorate, a much greater rate of extinction will occur in the near future.

The principal cause of decline, at least of the species in these families, is the outright loss or severe alteration of their habitat (table 4). The grazing and browsing of feral animals is perhaps the next greatest cause of destruction, as is shown here and outlined in the previous section on an island-by-island basis. Beyond these very obvious reasons for the deterioration of the Hawaiian flora, the myriad of other problems perhaps only touched upon in this analysis are much less obvious and usually more difficult to assess. For example, we presume that the original bird pollinators of species such as Erythrina sandwicensis and species of Hibiscadelphus are rare or extinct. Most of our present knowledge of pollination mechanisms is based primarily on floral morphology; direct observational studies are almost entirely lacking. We have suggested that there may be inbreeding depression resulting from extreme reduction of population size in plants such as Amaranthus brownii; however, there may be a dormant seed pool which could dramatically increase the population size in a favorable year. Again, we lack data that contribute to understanding the situation. Another problem requiring detailed study is the interaction between introduced insects and native plants. For example, the black twig borer, Xylosandrus compactus, is known to be a problem on many native plants such as Neowawraea phyllanthoides (Samuelson 1981; Howarth, this volume). This pest apparently was introduced prior to 1931, when H.L. Lyon collected it on elderberry plants imported from Singapore; 30 years later the species was collected again and was obviously spreading onto native plants (Samuelson 1981). Situations in which native insects are herbivorous on native plants, such as the insects that attack the young tender growth and meristems of Charpentiera species, are especially important to understand. We do not know if these situations are naturally cyclic or result from ecological imbalances triggered by perturbations of the ecosystems. The detection of some of these problems requires the careful, detailed field studies that are critically needed for most Hawaiian plants.

Another problem requiring detailed, long-term study is the dynamics of populations composed of native and alien species. The successional sequence that commences after a catastrophic event such as Hurricane Iwa, which hit Kaua'i in November 1982 and devastated a large portion of the koa forests in the Koke'e area, is unknown. Fast-growing naturalized species such as Passiflora mollissima and Rubus argutus that rapidly invade newly opened areas may largely replace the numerous koa seedlings that have begun to grow in devastated areas. The Hurricane has provided a rare opportunity for study.

Rain forest ecosystems have not been as greatly altered as other ecosystems and they are currently declining at a slower rate. If present land use practices and associated threats continue, however, these montane communities undoubtedly will ultimately suffer the same fate as lower elevation ecosystems. Although many rain forest species are currently "stable" or appear to have slow rates of decline, many others have been more severely affected. For example, some rain forest species of Campanulaceae are already extinct, such as Cyanea giffardii, which previously occurred only in low elevation rain forest near Glenwood on the windward slope of Kilauea, Hawai'i, and apparently was eliminated by development. Other problems contributing to the decrease in the number of many Campanulaceae include rats that girdle the soft woody stems, overcollection of certain rare taxa, and possibly genetic inbreeding. The invasion of many rain forest areas by feral pigs rapidly contributes to the degradation of the whole ecosystem through rooting activities, opening the habitat for alien species, and dispersing certain alien plants. Another Campanulaceae genus, Delissea, was rare and, for reasons that are unclear, was apparently already declining at the time of its original discovery.

HISTORY OF THE FLORA OF 'EWA PLAINS

Unless otherwise indicated, the information presented here was adapted from the 'Ewa Plains botanical survey by Chay and Balakrishnan (1979). This work is an unpublished report prepared for the U.S. Fish and Wildlife Service to map and census the rare and endangered plant species found on the 'Ewa coastal plains.

Setting and History

'Ewa Plains is located on the southwestern, leeward side of the island of O'ahu. It is bounded on the west and south by the Pacific Ocean, the east by Pearl Harbor, and the north by the southern end of the Wai'anae Mountains and the Schofield Plateau. The Plains extend from sea level to an elevation of 30 m, 6-8 km inland. The area lies in the rain shadow of the Ko'olau Mountains and has an average annual rainfall of 508 mm, most of it from southerly kona and winter storms. As a result, the climate has been classified as summer drought, an arid climatic condition characterized by long dry periods interrupted by periods of rain. The mean annual temperature ranges between 22.2 and 25.5 C with a relative humidity range of 60-70% (Kartawinata and Mueller-Dombois 1972; Richmond and Mueller-Dombois 1972).

The Plains were formed during the Pleistocene when the rise and fall of sea levels, which fluctuated approximately 120 m (Gascoyne, Benjamin and Schwarcz 1979), alternately created, flooded and exposed fringing coral reefs, allowing the valleys to cut into the exposed reefs. They are composed of a hard but extremely permeable calcareous substrate with deposited erosional products from the Wai'anae Mountains.

The Hawaiian Islands were first occupied by prehistoric settlers as early as 1,600 years ago (Kirch 1982). The eastern, Pearl Harbor end of 'Ewa Plains was populated and was a center for aquacultural activities as well as inshore fishing (Handy and Handy 1972). The western, Barbers Point area was sparsely settled, primarily by transient or seasonal fishing populations originating from the Pearl Harbor area. However, long-term or permanent occupation of the same area has been suggested by recent archaeological finds at a number of sites, and some subsistence agriculture may have been practiced. Dates of basaltic-glass samples from 2 cultural sites from this area yielded dates of 1612-1650 A.D. +/- 30 years (Sinoto 1978).

The area was observed by Western man very early in the historical period (Vancouver 1801). By the mid-1800's, it was occupied by a number of cattle ranches. The drilling of the first artesian well on O'ahu in Honouliuli in 1879, in conjunction with the construction of a rail line from Honolulu to western O'ahu in 1888, encouraged further settlement of 'Ewa Plains. In 1890, the 'Ewa Sugar Plantation was started and in 1893 a 20,000-plant sisal (Agave sisalana) plantation was started. By the mid 1920's the area contained many truck farms, piggeries, poultry farms, and a coconut plantation.

Military development began first with a mooring station for airships in the 1930's and continued with upgrading the facilities to include an airstrip and support structures. By the 1950's the area contained an airbase, an ammunition facility, and military housing and covered nearly 33% of the Plains area.

By the 1970's, besides the presence of the military and agricultural development, the area also contained several tracts of residential housing, quarries, recreational, commercial, and industrial areas, including an oil refinery. Today, agriculture and occupied land cover 88% of 'Ewa Plains, of which sugar cane fields occupy 36%; military lands, 33%; and 19% is composed of residential, recreational, and commercial areas and agriculture other than sugar. The remaining 12% of the Plains still contains native species in highly modified ecosystems.

The Flora of 'Ewa Plains

'Ewa Plains is an example of an area where the flora has been drastically changed by the alteration of natural ecosystems. The pre-contact flora of this area and others like it is not well known. However, a flora can be reconstructed from observations and collections from the remnant populations of native plants from Barbers Point and other similar areas (table 5). Corroborative evidence from the analysis of fossil snails also gives credence to the reconstruction (Christensen and Kirch, in prep.).

There is some question as to how extensively prehistoric Hawaiians altered the native 'Ewa Plains flora. Direct evidence from descriptions and collections of the area from this period is lacking, as in most places in Hawai'i. However, indirect evidence from archaeological and faunal finds suggests that prehistoric man might have had a substantial impact.

The species composition of land snails may serve as an indicator of the type of environment that existed in an area (Kerney 1966; Evans 1972; Bobrowsky 1984). Recent archaeological excavations conducted in the Barbers Point area have yielded an abundance of avian and terrestrial molluscan remains (Olson and James 1982; Sinoto 1978), many of which were extinct (Olson and James 1982; Christensen and Kirch, in prep.). Changes in species composition of the snail and avifauna found in pre-man, pre-Cook, and historic archaeological strata have suggested that these animals may

Table 5. Reconstruction of the major elements of the flora of 'Ewa Plains.[1]

Coralline area strand vegetation	
Achyranthes splendens var. *rotundata*	*Myoporum sandwicense* var. *stellatum*
Fimbristylis pycnocephala	*Portulaca cyanosperma*
Jacquemontia sandwicensis	*Sesuvium portulacastrum*
Lycium sandwicense	
Sand dunes strand vegetation	
Cuscuta sandwichiana	*Scaevola taccada*
Heliotropium anomalum var. *argenteum*	*Sida fallax*
Heliotropium curassavicum	*Sporobolus virginicus*
Ipomoea pes-caprae	*Tribulus cistoides*
Nama sandwicensis	*Vitex ovata*
Scaevola coriacea	
Estuaries and marshes	
Bacopa monnieria	*Scirpus paludosus*
Cyperus laevigatus	*Scirpus validus*
Inland open savannah - dryland sclerophyll forest	
Abutilon incanum	*Myoporum sandwicense*
Canavalia spp.	*Ophioglossum concinnum*
Capparis sandwichiana	*Panicum* spp.
Cassytha filiformis	*Panicum torridum*
Cocculus ferrandianus	*Plumbago zeylanica*
Eragrostis paupera	*Santalum ellipticum*
Erythrina sandwicensis	*Santalum freycinetianum*
Gossypium sandvicense	*Sapindus oahuensis*
Heteropogon contortus	*Sicyos microcarpus*
Ipomoea congesta	*Sida* spp.
Marsilea villosa	

[1] Summarized from Char and Balakrishnan (1979).

have become extinct prior to the arrival of Cook in 1778.

This evidence suggests that the composition of the indigenous flora may have been more substantially altered by prehistoric man than previously thought (Kirch 1982, 1983; Christensen and Kirch, in prep.). Evidence of such changes also can be found in numerous other areas of Hawai'i and Polynesia (Kirch 1982, 1983). The reconstruction of the native flora of the 'Ewa Plains area and similar strand and dryland sclerophyll forests suggests that some plants were useful to the natives (Rock 1913; Hatheway 1952; Char and Balakrishnan 1979). Moreover, the practice by the Hawaiians and other Pacific cultures of extensive clearing by burning may have occurred here (Kirch 1982). Clearing may have allowed naturalized plant species brought intentionally or unintentionally by settlers to establish themselves.

The historical changes in the flora are more easily documented. In their vegetation survey, Char and Balakrishnan (1979) found that of 396 species of vascular plants recorded, 347 or 88% were introduced and of the 49 that were native, 17 were endemic.

The present strand vegetation is dominated by the introduced Cynodon dactylon and the native Sporobolus virginicus, both of which grow well in disturbed areas. Native strand species such as Ipomoea imperati, I. pes-caprae, Tribulus cistoides, Sesuvium portulacastrum, Vitex ovata, and Scaevola taccada still occur in less disturbed areas. The range of these native strand species, however, has been decreased considerably due to the elimination of populations by clearing areas for housing and recreational sites.

The wetland areas near Pearl Harbor, once covered with Scirpus sp. and Bacopa monnieria, are slowly being dominated by mangrove (Rhizophora mangle), introduced in 1902 (Neal 1965). Above the mangrove is Batis maritima followed by the Polynesian-introduced Thespesia populnea and the presumably native Hibiscus tiliaceus. Along the margins of the strand and wetland areas, Pluchea indica and P. symphytifolia and their hybrid (P. xfosbergii) can be found.

The inland ecosystems have been more severely disturbed than the strand areas. The introduction of cattle in the middle 1800's aided in dispersing Prosopis pallida throughout the area, where it has since become the dominant tree. Localized sisal and coconut plants remain as remnants of now defunct sisal and coconut plantations. The shrub Leucaena leucocephala forms dense thickets along roadsides and a sub-canopy layer in Prosopis forests. These plants, along with Acacia farnesiana, Pithecellobium dulce, and Schinus terebinthifolius, are the dominant shrubs in open savannahs. Marsilea villosa in the past was one of the common groundcover plants in the Prosopis pallida forests, but this species now has been replaced by grasses such as Setaria verticillata. Pennisetum setosum and Chloris inflata can be found in recently disturbed areas. Sida fallax, Malvastrum coromandelianum, and Asystasia gangetica also occur in localized areas.

Native species such as Capparis sandwichiana, Myoporum sandwicense, and Chamaesyce skottsbergii var. kalaeloana are very localized. Others such as Santalum ellipticum, Sapindus oahuensis, and Gossypium sandvicense are rare. Other plants like Chamaesyce skottsbergii var. skottsbergii and Scaevola coriacea were not collected by Char and Balakrishnan (1979), although these species occurred there in the past. These species which probably were found throughout the inland plains area evidently have decreased considerably in their ranges.

Sugar cane now is the dominant species in the area and is intensively cultivated. Clearing natural areas for cane fields causes substantial disturbance to the native ecosystem. The substrate is further modified by agricultural byproducts for soil improvement and by water used in irrigation. The change in the growing conditions, caused by the absence of trees, additional soil and moisture, and soil improvements, perhaps enabled alien species to colonize the area instead of the original native plants. Further encroachment on the range of native species occurred when large tracts of land were covered by residential, industrial, and military sites, as discussed above.

The history of the flora of 'Ewa Plains illustrates what has happened to the native strand and dry sclerophyll forests in Hawai'i. Although precise dates are not available, it is clear that the changes occurred within the tenure of man's occupation. The emerging archaeological evidence from land snail and avifaunal analyses indicates the increasing role of prehistoric man in the acceleration of the modification of species composition and range to an area. This change was accelerated by several orders of magnitude with the arrival of modern man and his technology.

RESEARCH AND MANAGEMENT NEEDS

The basic requirement for the preservation of the Hawaiian flora is conservation of native communities by developing natural area protection policies and then setting up an adequate network of ecosystem reserves in all of our vegetation types. It is essential to have adequate research and education to successfully implement conservation policies. We also desperately need a modern flora to have a scientific basis for understanding individual groups. It has been nearly a century since the last complete flora of Hawai'i was published (Hillebrand 1888). This leaves the Hawaiian flora, which doubtless is one of the most interesting in the United States, without any significant modern inventory of its plants. As we have outlined above, the situation in Hawai'i is critical; thus a modern flora is viewed as one of the principal research priorities for further study of the Hawaiian flora.

A project initiated in 1982 by S.H. Sohmer and funded by the Irwin Charity Foundation of San Francisco is now under way at the Bishop Museum to produce such a modern framework. Manual of the Flowering Plants of Hawai'i will form a firm basis on which much-needed in-depth studies of specific groups of Hawaiian plants can be made. The philosophy of the Manual is to bring together, with a uniform treatment, the existing knowledge of the native flora pertinent to their identification, classification, distribution, and status. The project also has sought knowledgeable specialists to contribute treatments of specific groups to the book and has encouraged scientists to initiate more detailed research programs on difficult Hawaiian genera. The completion of this project will be a significant step towards an overall evaluation of our native flora; however, it should be followed by more detailed systematic studies as well as studies of pollination ecology, autecology, physiological ecology, genetics, and population biology. The Manual will be a single volume manual to the flowering plants of the Hawaiian Archipelago. It will contain keys and descriptions of the families, genera, and species, both native and naturalized, occurring throughout the Islands. The treatment of each species will include accepted scientific name, Hawaiian and English common names, list of synonyms, literature citations for relevant publications, statement of geographical and ecological ranges, available chromosome numbers, and brief notes on taxonomic problems. The principal source of information for this project is the approximately 70,000 specimens in the Hawaiian section of the herbarium at Bishop Museum; but the field knowledge of the authors, a large number of participating local botanists, and knowledgeable specialists of specific groups will also be incorporated.

The majority of studies made during the past 100 years on the Hawaiian flora has been based principally on descriptive taxonomy. Recently a number of detailed studies of cytology and experimental hybridization (Carr 1977, 1978; Carr and Kyhos 1981; Gardner 1976, 1977, 1979; Gillett 1966; Gillett and Lim 1970; T.

Lowrey, unpubl. data; Rabakonandrianina 1980; Rabakonandrianina and Carr 1981) have shed new insight into our understanding of genera such as Dubautia, Bidens, Scaevola, Tetramolopium, and Lipochaeta, and have provided examples of adaptive radiation patterns in Hawaiian plants. Physiological ecological studies such as those on Chamaesyce and Scaevola (Pearcy, Osteryoung, and Randall 1982; Pearcy 1983; Robichaux and Pearcy 1980a, 1980b, 1984) or studies of ecological distribution of C_3 and C_4 grasses (Rundel 1980) are very important in gaining insight on the ecological tolerances of different plant species, and thus shedding some light on how closely related organisms have adapted to and function in their habitat. Studies of comparative anatomy by Carlquist on a variety of Hawaiian plants (1957a, 1957b, 1959, 1962; Carlquist and Bissing 1976) and Stemmermann on Santalum (1980), as well as research on developmental anatomy by Herbst on Chamaesyce (1971, 1972), also have been valuable in understanding adaptation. Techniques for studying variation in proteins, such as the use of gel electrophoresis, are just beginning to be applied to Hawaiian plants, such as for Tetramolopium (T. Lowrey, unpubl. data). Population genetic and autecological studies, particularly regarding inbreeding suppression, are needed.

Studies of population dynamics and community level interactions are perhaps of even greater importance in the conservation of the native flora. For example, quantitative analysis of the impact of goats on various plants such as koa (Spatz and Mueller-Dombois 1973) and Sophora (Scowcroft and Giffin 1983; Scowcroft and Sakai 1983), and exclosure studies (Mueller-Dombois 1981) are critical in understanding the full effects of feral animals. Even more important are multidisciplinary studies directed towards understanding the structure and function of Hawaiian ecosystems. The U.S. International Biological Program (IBP) Island Ecosystems project (Mueller-Dombois, Bridges, and Carson 1981) used a team approach to study the structural biological organization in certain natural ecosystems in Hawai'i.

The following points can be made in summary of overall priorities and research needs (see also Smith, this volume).

1. Public education is essential to the acceptance of the concept of conservation and preservation of plant species. Education must be the foundation upon which all of our efforts are built. Only with long-term financial commitment that would result from such acceptance can a serious commitment be made to preservation (Raven 1976).

2. We must have a complete review of the native and naturalized plants of Hawai'i, such as the Flora

Project currently under way at the Bishop Museum. We also need local field surveys of specific areas such as those made by the Nature Conservancy of Hawai'i and Haleakala National Park (e.g., A.C. Medeiros, unpubl. data) and the Hawaiian Forest Bird Survey (Jacobi and Scott, this volume).

3. We have an immediate and critical need to establish through legislation and maintain through enforcement natural or semi-natural areas in as many of the native ecosystems of the Islands as possible. Excellent examples of this type of endeavor are Hawai'i Volcanoes National Park, Haleakala National Park, and The Nature Conservancy preserves.

4. Detailed biosystematic and ecological studies should be performed on carefully selected groups of organisms and communities. Especially critical for Hawaiian plants are studies of pollination ecology, for which we presently have extremely little information, and studies of demography and autecology of individual organisms, which are essential in seeking explanations for the requirements, tolerances, and responses in a community of organisms. Studies of physiological ecology are very important in gaining insight into the tolerances of plant species and how the organisms function and have adapted to their environments. These studies are of special importance, since they are concerned with the documentation and explanation of changes in the number of individuals and phenotypic and genotypic changes in populations over time. The information obtained is essential in the development of predictive models that can be used to implement successful management programs and to understand plant species and the communities that they comprise; it is fundamental to the overall study of any ecosystem.

5. Interactions between field biologists and horticulturists are very important in situations in which many species face imminent extinction. Botanical gardens form a network in which materials can be cultivated, propagated, and distributed to various other cultivation sites and perhaps can be reintroduced to native ecosystems. Interactions between horticulturists can lead to the development of new methods of cultivation. This kind of interaction seems to be especially fruitful in Hawai'i with the relatively large number of botanical gardens.

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LITERATURE CITED

Armstrong, R.W., ed. 1973. Atlas of Hawaii. Honolulu: Univ. Pr. Hawaii.

Bobrowsky, P.T. 1984. The history and science of gastropods in archaeology. Am. Antiquity 49:77-93.

Campbell, D.H. 1920. Some botanical and environmental aspects of Hawaii. Ecology 1:257-269.

Carlquist, S. 1957a. Systematic anatomy of Hesperomannia. Pac. Sci. 11:207-215.

Carlquist, S. 1957b. Leaf anatomy and ontogeny in Argyroxiphium and Wilkesia (Compositae). Am. J. Bot. 44:696-705.

Carlquist, S. 1959. Studies on Madinae: anatomy, cytology, and evolutionary relationships. Aliso 4:171-236.

Carlquist, S. 1962. Ontogeny and comparative anatomy of thorns of Hawaiian Lobeliaceae. Am. J. Bot. 49:413-419.

Carlquist, S. 1974. Island biology. New York: Columbia Univ. Pr.

Carlquist, S., and D.R. Bissing. 1976. Leaf anatomy of Hawaiian geraniums in relation to ecology and taxonomy. Biotropica 8:248-259.

Carr, G.D. 1977. Cytogenetics of Hibiscadelphus (Malvaceae): a meiotic analysis of hybrids in Hawaii Volcanoes National Park. Pac. Sci. 31:191-194.

Carr, G.D. 1978. Hybridization in the Hawaiian silversword complex. Proc. 2nd Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 37-40. Honolulu: Univ. Hawaii.

Carr, G.D. 1981a. Status report on Santalum freycinetianum Gaud. var. lanaiense Rock. U.S. Fish Wildl. Serv., Honolulu. Typescript.

Carr, G.D. 1981b. Status report on Argyroxiphium sandwicense DC. var. sandwicense. U.S. Fish Wildl. Serv., Honolulu. Typescript.

Carr, G.D. 1981c. Status report on Scaevola coriacea Nutt. U.S. Fish Wildl. Serv., Honolulu. Typescript.

Carr, G.D., and D.W. Kyhos. 1981. Adaptive radiation in the Hawaiian silversword alliance (Compositae-Madiinae). I. Cytogenetics of spontaneous hybrids. Evolution 35:543-556.

Char, W.P., and N. Balakrishnan. 1979. Ewa plains botanical survey. U.S. Fish Wildl. Serv., Honolulu. Typescript.

Christensen, C.C., and P.V. Kirch. In prep. Nonmarine mollusks and ecological change at Barbers Point, Oahu, Hawaii. B.P. Bishop Mus.

Clark, J.T., and P.V. Kirch, eds. 1983. Archaeological investigations of the Mudlane-Waimea-Kawaihae road corridor, island of Hawaii: an interdisciplinary study of an environmental transect. B.P. Bishop Mus. Dep. Anthropol. Rep. Ser. 83-1.

Dalrymple, G.B., M.A. Lanphere, and E.D. Jackson. 1974. Contributions to the petrography and geochronology of volcanic rocks from the leeward Hawaiian Islands. Geol. Soc. Am. Bull. 85:727-738.

Degener, O., and I. Degener. 1975. Review of list of flowering plants in Hawaii by H. St. John. Sida 6:120-122.

Egler, F.E. 1939. Vegetation zones on Oahu, Hawaii. Empire For. Rev. 8:44-57.

Evans, J.G. 1972. Land snails in archaeology. London: Seminar Pr.

Fay, J. 1979. Endangered and threatened wildlife and plants; determination that Kokia cookei is an endangered species. Fed. Register 44(211): 62470-62471.

Fay, J. 1980. Endangered and threatened wildlife and plants; proposed endangered status for the Ewa Plains akoko (Euphorbia skottsbergii var. kalaeloana). Fed. Register 45(171):58166-58168.

Fay, J. 1982. Endangered and threatened wildlife and plants; determination that Euphorbia skottsbergii var. kalaeloana (Ewa Plains akoko) is an endangered species. Fed. Register 47(164): 36846-36849.

Forbes, C.N. 1913. An enumeration of Niihau plants. B.P. Bishop Mus. Occ. Pap. 5:99-108.

Fosberg, F.R. 1948. Derivation of the flora of the Hawaiian Islands. In Insects of Hawaii, ed. E.C. Zimmerman, Vol. 1, Introduction, 107-119. Honolulu: Univ. Hawaii Pr.

Fosberg. F.R. 1972. Guide to Excursion III. In Tenth Pacific Science Congress, rev. ed. Honolulu: Univ. Hawaii.

Fosberg, F.R., and D.R. Herbst. 1975. Rare and endangered species of Hawaiian vascular plants. Allertonia 1:1-72.

Funk, E.J., and C.W. Smith. 1982. Status report on Abutilon menziesii Seem. U.S. Fish Wildl. Serv., Honolulu. Typescript.

Gagne, B.H. 1982. Status report on Gardenia brighamii Mann. U.S. Fish Wildl. Serv., Honolulu. Typescript.

Gagne, W.C., and D. Mueller-Dombois. n.d. Synopsis of terrestrial vegetation types. B.P. Bishop Mus. and Univ. Hawaii Dep. Bot. Typescript.

Gardner, R.C. 1976. Evolution and adaptive radiation in Lipochaeta (Compositae) of the Hawaiian Islands. Syst. Bot. 1:383-391.

Gardner, R.C. 1977. Chromosome numbers and their systematic implications in Lipochaeta (Compositae: Heliantheae). Am. J. Bot. 64:810-813.

Gardner, R.C. 1979. Revision of Lipochaeta (Compositae: Heliantheae) of the Hawaiian Islands. Rhodora 81:291-343.

Gascoyne, M., G.J. Benjamin, and H.P. Schwarcz. 1979. Sea-level lowering during the Illinoian glaciation: evidence from a Bahama "blue hole." Science 205:806-808.

Gillett, G.W. 1966. Hybridization and its taxonomic implications in the Scaevola gaudichaudiana complex of the Hawaiian Islands. Evolution 20:206-216.

Gillett, G.W., and E.K.S. Lim. 1970. An experimental study of the genus Bidens (Asteraceae) in the Hawaiian Islands. Univ. Calif. Pub. Bot. 56.

Handy, E.S., and E.G. Handy. 1972. Native planters in old Hawaii, their life, lore, and environment. B.P. Bishop Mus. Bull. 233.

Hara, A.H., and J.W. Beardsley, Jr. 1979. The biology of the black twig borer, Xylosandrus compactus (Eichhoff), in Hawaii. Proc. Hawaii. Entomol. Soc. 23:55-70.

Hatheway, W.H. 1952. Composition of certain native dry forests: Mokuleia, Oahu, T.H. Ecol. Monogr. 22:153-168.

Herbst, D.R. 1971. Disjunct foliar veins in Hawaiian euphorbias. Science 171:1247-1248.

Herbst, D.R. 1972. Ontogeny of foliar venation in Euphorbia forbesii. Am. J. Bot. 59:843-850.

Herbst, D.R. 1978. Status report on Hibiscadelphus distans Bishop and Herbst. U.S. Fish Wildl. Serv., Honolulu. Typescript.

Herbst, D.R. 1979. Status report on Remya mauiensis Hbd. U.S. Fish Wildl. Serv., Honolulu. Typescript.

Herbst, D.R. 1983a. Endangered and threatened wildlife and plants; proposed endangered status and critical habitat for Gouania hillebrandii. Fed. Register 48(174):40407-40411.

Herbst, D.R. 1983b. Endangered and threatened wildlife and plants; proposed endangered status and critical habitat for Kokia drynarioides (hauhele ula). Fed. Register 48(177):40920-40923.

Herbst, D.R. 1984. Endangered and threatened wildlife and plants; final rule to list Bidens cuneata and Schiedea adamantis as endangered species. Fed. Register 49(34):6099-6101.

Herbst, D.R., and J. Fay. 1979. Endangered and threatened wildlife and plants; determination that three Hawaiian plants are endangered species. Fed. Register 44(211):62468-62469.

Herbst, D.R., and J. Fay. 1981. Endangered and threatened wildlife and plants; proposal to list Panicum carteri (Carter's panicgrass) as an endangered species and determine its critical habitat. Fed. Register 46(20):9976-9979.

Herbst, D.R., and J. Fay. 1983. Endangered and threatened wildlife and plants; rule to list Panicum carteri (Carter's panicgrass) as an endangered species and determine its critical habitat. Fed. Register 48(198):46328-46332.

Herbst, D.R., and W. Takeuchi. 1982. Endangered and threatened wildlife and plants; proposed endangered status for Bidens cuneata and Schiedea adamantis. Fed. Register 47(163):36675-36678.

Hillebrand, W. [1888] 1981. Flora of the Hawaiian Islands: a description of their phanerogams and vascular cryptogams. Facsimile. Monticello, New York: Lubrecht and Cramer.

Hobdy, R.W. 1984. A re-evaluation of the genus Hibiscadelphus (Malvaceae) and the description of a new species. B.P. Bishop Mus. Occ. Pap. 25(11):1-7.

Holt, R.A., and B. Fox. Protection status of the native Hawaiian biota. [This volume]

Howarth, F.G. Impacts of alien land arthropods and mollusks on native plants and animals in Hawaii. [This volume]

Jacobi, J.D., and J.M. Scott. An assessment of the current status of native upland habitats and associated endangered species on the island of Hawaii. [This volume]

Kartawinata, K., and D. Mueller-Dombois. 1972. Phytosociology and ecology of the natural dry-grass communities on Oahu, Hawaii. Reinwardtia 8:369-494.

Kerney, M.P. 1966. Snails and man in Britain. J. Conchol. 26:3-14.

Kirch, P.V. 1982. The impact of the prehistoric Polynesians on the Hawaiian ecosystem. Pac. Sci. 36:1-14.

Kirch, P.V. 1983. Man's role in modifying tropical and subtropical Polynesian ecosystems. Archaeol. Oceania 18:26-31.

Knapp, R. 1965. Die vegetation von Nord- und Mittelamerika und der Hawaii-Inseln. Stuttgart, Germany: Fisher. [Translated and published in Hawaii. Bot. Soc. Newsl. 14(5):95-121. 1975.]

Krajina, V.J. 1963. Biogeoclimatic zones of the Hawaiian Islands. Hawaii. Bot. Soc. Newsl. 2:93-98.

Lamoureux, C. 1963. The flora and vegetation of Laysan Island. Atoll Res. Bull. 97.

Lamoureux, C. 1982. Status report on *Mezoneuron kavaiense* (Mann) Hbd. U.S. Fish Wildl. Serv., Honolulu. Typescript.

Lassetter, J.S., and C.R. Gunn. 1979 [1980]. *Vicia menziesii* Sprengel (Fabaceae) rediscovered: its taxonomic relationships. *Pac. Sci.* 33:85-101.

Leeper, J.R., and J.W. Beardsley. 1973. *The bioecology of* Psylla uncatoides *in the Hawaii Volcanoes National Park and the* Acacia koaia *sanctuary.* U.S. Internatl. Biol. Prog. Island Ecosys. Tech. Rep. 23. Honolulu: Univ. Hawaii.

Lucas, G., and H. Synge, eds. 1977. *The IUCN plant red data book*. Morges, Switzerland: Internatl. Union Conserv. Nat. and Nat. Resour.

McManus, R.E., R.F. Altevogt, and B. MacBryde. 1978. Endangered and threatened wildlife and plants; determination that 11 plant taxa are endangered species and 2 plant taxa are threatened species. *Fed. Register* 43(81):17910-17916.

Morgan, W.J. 1972. Deep mantle convection pluves and plate motions. *Am. Assn. Petroleum Geol. Bull.* 56:203-213.

Mueller-Dombois, D. 1981. Vegetation dynamics in a coastal grassland of Hawaii. *Vegetatio* 46: 131-140.

Mueller-Dombois, D. Ohia dieback and protection management of the Hawaiian rain forest. [This volume]

Mueller-Dombois, D., and V. J. Krajina. 1968. Comparison of east-flank vegetation on Mauna Loa and Mauna Kea, Hawaii. In *Recent advances in tropical ecology 2*, ed. R. Misra and B. Gopal, 508-520. Internatl. Soc. Trop. Ecol. Benares Hindu Univ.

Mueller-Dombois, D., and G. Spatz. 1972. *The influence of feral goats on the lowland vegetation in Hawaii Volcanoes National Park.* U.S. Internatl. Biol. Prog. Island Ecosys. Tech. Rep. 13. Honolulu: Univ. Hawaii.

Mueller-Dombois, D., K.W. Bridges, and H.L. Carson, eds. 1981. *Island ecosystems: biological organization in selected Hawaiian communities.* Stroudsburg, Penn.: Hutchinson Ross Pub. Co.

Nagata, K.M. 1981. Status report on *Achyranthes rotundata* (Hbd.) St. John. U.S. Fish Wildl. Serv., Honolulu. Typescript.

Neal, M.C. 1965. *In gardens of Hawaii*. B.P. Bishop Mus. Spec. Pub. 50.

Obata, J.K., and C.W. Smith. 1981. Status report on *Cyanea superba* (Cham.) A. Gray. U.S. Fish Wildl. Serv., Honolulu. Typescript.

Olson, S.L., and H.F. James. 1982. *Prodromus of the fossil avifauna of the Hawaiian Islands.* Smithson. Contrib. Zool. 365.

Pearcy, R.W. 1983. The light environment and growth of C_3 and C_4 tree species in the understory of a Hawaiian forest. *Oecologia* 58:19-25.

Pearcy, R.W., K. Osteryoung, and D. Randall. 1982. Carbon dioxide exchange characteristics of C_4 Hawaiian *Euphorbia* species native to diverse habitats. *Oecologia* 55:333-341.

Rabakonandrianina, E. 1980 [1981]. Infrageneric relationships and the origin of the Hawaiian endemic genus *Lipochaeta* (Compositae). *Pac. Sci.* 34:29-39.

Rabakonandrianina, E., and G.D. Carr. 1981. Intergeneric hybridization, induced polyploidy, and the origin of the Hawaiian endemic *Lipochaeta* from *Wedelia* (Compositae). *Am. J. Bot.* 68:206-215.

Ralph, C.J., A.P. Pearson, and D.C. Phillips. 1980 [1981]. Observations on the life history of the endangered Hawaiian vetch (*Vicia menziesii*) (Fabaceae) and its use by birds. *Pac. Sci.* 34:83-92.

Raven, P.H. 1976. Ethics and attitudes. In *Conservation of threatened plants*, ed. J.B. Simmons, R.I. Beyer, P.E. Brandham, G. L. Lucas, and V.T. Parry, 155-179. New York: Plenum Pr.

Richmond, T. de A., and D. Mueller-Dombois. 1972. Coastline ecosystems on Oahu, Hawaii. *Vegetatio* 25:367-400.

Ripperton, J.C., and E.Y. Hosaka. 1942. *Vegetation zones of Hawaii.* Hawaii Agric. Exp. Stn. Bull. 89.

Robichaux, R.H., and R.W. Pearcy. 1980a. Environmental characteristics, field water relations, and photosynthetic responses of C_4 Hawaiian Euphorbia species from contrasting habitats. Oecologia 47:99-105.

Robichaux, R.H., and R.W. Pearcy. 1980b. Photosynthetic responses of C_3 and C_4 species from cool shaded habitats in Hawaii. Oecologia 47:106-109.

Robichaux, R.H., and R.W. Pearcy. 1984. Evolution of C_3 and C_4 plants along an environmental moisture gradient: patterns of photosynthetic differentiation in Hawaiian Scaevola and Euphorbia species. Am. J. Bot. 71:121-129.

Rock, J.F. [1913] 1974. The indigenous trees of the Hawaiian Islands. Reprint, with Introduction by S. Carlquist and Addenda by D.R. Herbst. Privately pub.

Rundel, P.W. 1980. The ecological distribution of C_4 and C_3 grasses in the Hawaiian Islands. Oecologia 45:354-359.

St. John, H. 1959. Botanical novelties on the island of Niihau, Hawaiian Islands. Hawaiian plant studies 25. Pac. Sci. 13:156-190.

St. John, H. 1966. Monograph of Cyrtandra (Gesneriaceae) on Oahu, Hawaiian Islands. B.P. Bishop Mus. Bull. 229.

St. John, H. 1973. List and summary of the flowering plants in the Hawaiian Islands. Pac. Trop. Bot. Gard. Mem. 1.

St. John, H. 1976. New species of Hawaiian plants collected by David Nelson in 1779. Hawaiian plant studies 52. Pac. Sci. 30:7-44.

St. John, H. 1978. The first collection of Hawaiian plants by David Nelson in 1779. Hawaiian plant studies 55. Pac. Sci. 32:315-324.

St. John, H. 1982. Vernacular plant names used on Niihau Island. Hawaiian plant studies 69. B.P. Bishop Mus. Occ. Pap. 25(3):1-10.

Samuelson, G.A. 1981. A synopsis of Hawaiian Xyleborini (Coleoptera: Scolytidae). Pac. Insects 23:50-92.

Schauinsland, H. 1899. Drei monate auf einter Korallen-Insel [Laysan]. Bremen: Max Nossler.

Scholl, D.W., and J.S. Creager. 1973. Geologic synthesis of Leg 19 (DSDP) results; for North Pacific, and Aleutian Ridge, and Bering Sea. In Initial reports of the deep sea drilling project 19, 897-913. La Jolla, Calif.: Scripps Inst. Oceanogr.

Scowcroft, P.G. 1983. Tree cover in mamane (Sophora chrysophylla) forests grazed by sheep and cattle. Pac. Sci. 37:109-119.

Scowcroft, P.G., and J.G. Giffin. 1983. Feral herbivores suppress mamane and other browse species on Mauna Kea, Hawaii. J. Range Manage. 36:638-645.

Scowcroft, P.G., and H. F. Sakai. 1983. Impact of feral herbivores on mamane forests of Mauna Kea, Hawaii: bark stripping and diameter class structure. J. Range Manage. 36:495-498.

Sinoto, A. 1978. Archaeological and paleontological salvage at Barbers Point, Oahu. B.P. Bishop Mus. Dep. Anthropol., Honolulu. Typescript.

Smith, C.W. Impact of alien plants on Hawaii's native biota. [This volume]

Spatz, G., and D. Mueller-Dombois. 1973. The influence of feral goats on koa tree reproduction in Hawaii Volcanoes National Park. Ecology 54:870-876.

Stein, J.D. 1983a. The biology, host range parasites, and hyperparasites of koa seed insects in Hawaii: a review. Proc. Hawaii. Entomol. Soc. 24:317-326.

Stein, J.D. 1983b. Insects associated with Acacia koa seed in Hawaii. Environ. Entomol. 12:299-302.

Stemmermann, R.L. 1980 [1981]. Vegetative anatomy of the Hawaiian species of Santalum (Santalaceae). Pac. Sci. 34:55-75.

Stone, C.P. Alien animals in Hawaii's native ecosystems: toward controlling the adverse effects of introduced vertebrates. [This volume]

Synge, H., ed. 1981. The biological aspects of rare plant conservation. New York: John Wiley Sons.

U.S. Fish and Wildlife Service. 1975. Endangered or threatened fauna or flora; review of status of vascular plants and determination of "critical habitat." Fed. Register 40(127):27824-27924.

U.S. Fish and Wildlife Service. 1976. Endangered and threatened wildlife and plants; proposed endangered status for some 1700 U.S. vascular plant taxa. Fed. Register 41(117):24523-24572.

U.S. Fish and Wildlife Service. 1980. Endangered and threatened wildlife and plants; review of plant taxa for listing as endangered or threatened species. Fed. Register 45(242):82480-82569.

Vancouver, G. 1801. A voyage of discovery to the North Pacific Ocean and round the world, 6 vol. London: John Stockdale.

Warshauer, F.R., and J.D. Jacobi. 1982. Distribution and status of Vicia menziesii Spreng. (Leguminosae): Hawaii's first officially listed endangered plant species. Biol. Conserv. 23:111-126.

Warshauer, F.R., J.D. Jacobi, A.M. La Rosa, J.M. Scott, and C.W. Smith. 1983. The distribution, impact and potential management of the introduced vine Passiflora mollissima (Passifloraceae) in Hawaii. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. 48. Honolulu: Univ. Hawaii.

Wester, L.L., and H.B. Wood. 1977. Koster's curse (Clidemia hirta), a weed pest in Hawaiian forests. Environ. Conserv. 4:35-41.

3.

DISTRIBUTION AND ABUNDANCE OF HAWAI'I'S ENDEMIC LAND BIRDS: CONSERVATION AND MANAGEMENT STRATEGIES

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ABSTRACT

Hawaiian forest birds are currently limited in habitat, diversity, range, and numbers by numerous past and present stresses. The 6-year U.S. Fish and Wildlife Service Hawaii Forest Bird Survey has provided information on status, distribution, habitat relationships, and many limiting factors. These are summarized for Hawaiian birds in this paper. In order to restore and maintain viable populations of Hawai'i's native birds, application of one or more of 6 management actions is necessary, depending on the seriousness or immediacy of the threat to the species or group of species. The actions are as follows: 1) Legal protection of natural habitats; 2) Elimination of introduced plants and animals in native habits; 3) Physical restoration of native habitats through reforestation; 4) Intensive manipulation of birds in natural habitats; 5) Translocation of endangered species; 6) Captive propagation. Specific management recommendations are made for a number of areas in Hawai'i. Cooperation with private landowners is emphasized.

INTRODUCTION

The native Hawaiian birds have suffered catastrophic losses since man arrived about 400 A.D. (Kirch 1982). Recent fossil evidence suggests that only 25% of the original taxa still survive (S.L. Olson, pers. comm.). A minimum of 40 species was lost in a first extinction wave induced by Polynesian man and his commensals. These losses were the result of widespread habitat destruction at elevations below 1,000 m (Kirch 1982), predation by introduced dogs and rats, and killing for food (Stone, this volume).

A second extinction wave began with the arrival of western man in 1778 and has continued unabated as newly introduced cattle (*Bos taurus*), goats (*Capra hircus*), and sheep (Ovis aries) placed added pressure on native forests. Many birds were lost in the 19th and early 20th century as mid-elevation mesic forests were converted to agricultural lands, and as introduced diseases and rats (Rattus rattus) spread into native forests (Atkinson 1977; Berger 1981). Introduced species acted as competitors (Mountainspring and Scott, in press), reservoirs for disease (Warner 1968; van Riper et al., in press; van Riper and van Riper, this volume), predators (Atkinson 1977), and severe modifiers of native habitats (Scott et al. 1984; Scott et al., in press; Warshauer et al. 1983). The effects of introduced species have continued into the late 20th century. These stresses, combined with direct habitat destruction by man and his commensals (Scott et al., in press), continue to place pressure on native birds, particularly those now restricted to ranges representing mere fractions of their former distributional areas. The history of the native Hawaiian avifauna has been and continues to be one of loss of diversity, numbers, and habitat.

Imagine a species that was found from the dry coastal woodlands to the dry subalpine shrublands at 3,000 m on Mauna Kea, and which reached its greatest numbers in the mid-elevation mesic forests. Its range was severely truncated with the loss of lowland habitat up to about 1,000 m as the result of Polynesian agricultural practices (Kirch 1982). Ungulates introduced by Captain Cook and others further degraded the remaining dry habitats and initiated the process in the middle and upper elevation moist and wet forests beginning in the early 19th century. The dramatic increase in predators in the 1800's and 1900's (Atkinson 1977) and the introduction of avian diseases during this same period resulted in further losses. The greatest impact of diseases was on birds restricted to elevations below 1,000 m (Warner 1968; van Riper et al., in press). In the 20th century further exploitation continued in the upland forests: the moist koa (Acacia koa)-'ohi'a (Metrosideros polymorpha) forests on Maui and Hawai'i, subjected to logging and cattle grazing, disappeared in many areas. Wet 'ohi'a forests were denuded by an expanding feral pig (Sus scrofa) population. Avian malaria may have been introduced for the first time in the 1930's (van Riper et al., in press), resulting in further declines in numbers of individuals. The end result, then, is a severely diminished range occupied with but a fraction of the pre-Polynesian population.

This scenario has been repeated over and over again. Many species have been lost, and those that remain occupy but a very small percentage of their original ranges. In some cases these are relict in the extreme. The po'ouli (Melamprosops phaeosoma), large

Kaua'i thrush (Phaeornis obscurus myadestina), and palila (Loxioides bailleui) occupy less than 10% of their historical ranges (Scott et al., in press). Work by 20th century ornithologists indicates that reduction in ranges and decreases in population sizes are continuing. The forest birds on Kaua'i and Moloka'i are perhaps the best examples that we have of this ongoing extinction process (Sincock et al. 1984; Scott et al., in press). However, additional examples can be found on Hawai'i. The 'akepa (Loxops coccineus coccineus) and Hawai'i creeper (Oreomystis mana) have disappeared from Hawai'i Volcanoes National Park, and the 'o'u (Psittirostra psittacea) has declined too. All this has occurred in the last 50 years.

Although there were many questions concerning distribution, abundance, and limiting factors of Hawai'i's birds in 1974, 30 Hawaiian birds were listed as endangered or threatened (U.S. Fish and Wildlife Service 1983). Public and private conservation agencies were justifiably reluctant to commit to major recovery efforts without solid information on where birds were found or what was responsible for their low numbers. During the 10 years that have elapsed, much new information has been obtained. Intensive studies were undertaken on the Hawaiian goose, Nesochen sandvicensis (Banko and Manuwal 1982), palila (van Riper 1978; van Riper, Scott, and Woodside 1978; Scott et al. 1984), Hawaiian hawk, Buteo solitarius (C. Griffin, unpubl. data), and Hawaiian crow, Corvus hawaiiensis (S.L. Temple, unpubl. data). Exhaustive surveys of Hawai'i, Maui, Moloka'i, Lana'i, Kaua'i, and parts of O'ahu were conducted (Scott et al., in press); Shallenberger and Vaughn 1978); a major effort to understand the role of disease was completed (van Riper et al., in press); and an extensive review of the literature (Banko 1980-1983) was conducted.

The status, distribution, habitat relationships, and many limiting factors for most of Hawai'i's native forest birds were extensively documented during the 6-year U.S. Fish and Wildlife Service (FWS) Hawaii Forest Bird Survey (HFBS) (Scott et al. 1984; Scott et al., in press). The HFBS data base, combined with those of the U.S. Forest Service (USFS), U.S. National Park Service (NPS), and others can be used to review the status and legal standing of a species, prioritize conservation efforts, and make management recommendations. Based on this documentation, specific management actions have been proposed for many species (Berger et al. 1977; Burr et al. 1982; Scott et al. 1983; Sincock et al. 1984; Kepler et al. 1984). If the proposed actions are implemented, the long-term survival chances of many endangered Hawaiian birds should be enhanced.

We are fully aware that the various stresses faced by avian species will cause the status of each to fluctuate, and that the continual influx of alien species of plants and animals introduces additional challenges to the long-term survival chances of native organisms (Smith, this volume; Howarth, this volume; Stone, this volume). With this in mind, we offer the following review of the status of native Hawaiian land birds.

SPECIES ACCOUNTS

Hawaiian Goose (*Nesochen sandvicensis*)

The Hawaiian goose, or nene, probably numbered fewer than 30 birds in 1951 (Smith 1952). A State and federally funded captive propagation effort was initiated in 1949. Two decades later the nene appeared to be recovering (Kear and Berger 1980; Stone et al. 1983). Recent surveys (Devick 1981a, 1981b), however, indicate that the population cannot be sustained without a release program. Possible explanations for the decline have been reviewed (Stone et al. 1983) and include predation and inadequate food. It has been suggested that the best and largest breeding areas of the nene formerly occurred in the lowlands, and that the upland parts of its range were marginal for breeding and rearing young (Henshaw 1902; Perkins 1903). It has been further suggested that habitat alteration and high predator densities have left the formerly suitable lowland areas incapable of supporting a self-sustaining nene population (Stone et al. 1983). Ongoing research is attempting to more precisely determine those factors that limit natural reproduction. For the present, the chances of survival of this species are secure through captive propagation. It remains to be determined if a wild population can be maintained without man's assistance.

Hawaiian Hawk (*Buteo solitarius*)

This species is resident only on Hawai'i. It is unique among Hawai'i's forest birds in that it is still found throughout almost all of its historical range (Scott et al., in press). It occurs in alien as well as native forests, feeding extensively on introduced vertebrates, and has no apparent reproductive problems (C. Griffin, unpubl. data). Although no population estimates are available, densities, distribution, and reproduction clearly indicate a healthy population in no danger of extinction. Observers should, however, continue to be aware of the threats posed by pesticides and especially herbicide applications.

Hawaiian Rail (*Porzana sandwichensis*)

This species is definitely known only from Hawai'i, although fossil evidence suggests that closely related flightless rails were found on the other large islands in historical times (Olson and James 1982). It was last seen on Hawai'i about 1884 (Berger 1981) and is considered extinct (Scott et al., in press).

Short-eared Owl (Asio flammeus sandwichensis)

Studies show well-established populations on all the main islands (Berger 1981). We know, however, almost nothing about reproduction and survival of this subspecies. The periodic but unexplained "die-offs" among the introduced common barn owl (Tyto alba) have not been recorded for short-eared owls (L. Pank, pers. comm.). Although Scott et al. (in press) found it in a wide variety of habitats on Hawai'i, Maui, Moloka'i, Lana'i, and Kaua'i, no attempts were made to estimate population sizes. Short-eared owls are less frequently seen on Hawai'i than the endangered Hawaiian hawk, probably because of behavioral differences.

Hawaiian Crow (Corvus hawaiiensis)

This is one of the rarest of the endemic Hawaiian species. Its population was estimated at 76 in 1978 (Scott et al., in press). Since that time it is known to have declined (Giffin 1983; J.G. Giffin, unpubl. data). The historical status of the crow was recently reviewed (Banko and Banko 1980; Scott et al., in press). Avian malaria has been found in captive and wild Hawaiian crows and is suspected to be a significant limiting factor (C. van Riper, pers. comm.).

The leeward forests of Kona where the crow is found are steadily declining in quality as crow habitat because of logging, grazing, and urban development. This development brings with it increased disturbance at nest sites and increased loss of birds through incidental shooting. Recent studies have indicated that the best remaining habitat is undisturbed koa-'ohi'a forest (J.G. Giffin, unpubl. data). While parts of State Conservation Districts in Kona are zoned "Preserve", "No prime habitat, no alala nest and only 1% of high grade secondary habitat fell within this subzone" (J.G. Giffin, unpubl. data). Recent logging operations in what is considered to be the center of the crow's range further threaten the long-term survival chances for this species. State and Federal biologists have embarked upon a conservation program (Burr et al. 1982).

'Elepaio (Chasiempsis sandwichensis)

This species is widespread and abundant on Hawai'i (200,000 birds) and Kaua'i (63,000) and uncommon on O'ahu. Two subspecies of 'elepaio on Hawai'i (C. s. ridgwayi and C. s. sandwichensis) appear to be healthy (Scott et al., in press). A third subspecies that was recently described, C. sandwichensis bryani (Pratt 1980), is found only in mamane (Sophora chrysophylla) and naio (*Myoporum sandwicense*) forest on Mauna Kea, where it occupies 70% of the range of the palila. The population size of *C. sandwichensis bryani*, 2,500, is similar to that of the endangered palila. The quality of mamane forest within 'elepaio range has improved with the recent removal of most of the feral sheep and goats (Scott et al. 1984). However, continued browsing and grazing by mouflon sheep (*Ovis musimon*), which are expanding their range, threaten to reverse the trend toward habitat improvement (Scowcroft and Giffin 1983; Giffin 1982; Scowcroft and Sakai 1983).

The occurrence of 'elepaio in the lowlands on windward Hawai'i, O'ahu, and Kaua'i suggests that this species may have evolved some resistance to diseases that are thought to limit the range and numbers of other Hawaiian species.

Hawaiian Thrush (*Phaeornis obscurus*)

Five subspecies of this bird are known from the Islands (Berger 1981). Although the subspecies on Hawai'i (*P. o. obscurus*) seems most secure, with a population estimated at 160,000 birds (Scott et al., in press), puzzling gaps in its distribution exist. It is almost totally absent from the leeward forests, and was extirpated from the windward forests of Kohala Mountain years ago (van Riper and Scott 1979; van Riper 1982; Scott et al., in press). On the bright side, high numbers have been recorded below 1,500 m in parts of the windward forests of the Puna and Hamakua coasts (Scott et al., in press). High numbers at lower elevations suggest that, as with the 'elepaio, some resistance to avian malaria and/or pox may be developing in those populations.

Intensive surveys in the late 1970's failed to locate any Hawaiian thrushes on Maui (Scott et al., in press). Recently found subfossil remains indicate that it commonly occurred there within the last 1,000 years (S.L. Olson, pers. comm.).

The Moloka'i subspecies (*P. o. rutha*) is extremely rare. Two individuals were observed in 1975 (Scott, Woodside, and Casey 1977). Estimates based on a recent survey indicate a population of 19 birds (Scott et al., in press). Acquisition and management of the 28 km^2 Kamakou Preserve by The Nature Conservancy increases the chances of long-term survival of prime habitat on Moloka'i. We are not, however, optimistic that such a small population, subjected to avian malaria and pox, can long survive.

The Kaua'i subspecies (*P. o. myadestina*) has declined steadily since the turn of the century (Sincock et al. 1984). Intensive coverage of its range resulted in a population estimate of 24 birds in 1981, down from 200 in 1968-75. This decline has occurred despite legal protection of its entire range and no obvious changes in habitat quality. Although a few birds may remain in areas outside those surveyed during the HFBS, chances for the long-term survival of a naturally reproducing population of P. o. myadestina seem bleak.

Small Kaua'i Thrush (Phaeornis palmeri)

The population of the small Kaua'i thrush from 1968-1973 was estimated at 100 in the heart of its range (Sincock et al. 1984). More recent surveys indicate a population of only 20 (Scott et al., in press). Two recently discovered nests have both resulted in young birds fledging (Kepler and Kepler 1983; Ashman, Pyle, and Jeffrey 1984). As with the Hawaiian thrush, a few birds may occur outside recently surveyed areas. However, the numbers and distribution of this species clearly indicate a population which is precariously small and declining (Scott et al., in press).

Kaua'i 'O'o (Moho braccatus)

Once common throughout Kaua'i, this species has undergone a steady decline since its rediscovery in 1960 (Richardson and Bowles 1964). Despite intensive searches, no indications of breeding activity have been noted since 1981 (J.L. Sincock, pers. comm.). Searches in the spring of 1983 and again in the fall of 1984 resulted in the observation of only one bird (presumably a male) in the Alaka'i Swamp (J.L. Sincock, pers. comm.). Unless heretofore unsuspected numbers of this species are found, it may be beyond the point where even a captive propagation effort could save it.

O'ahu 'O'o (Moho apicalis)

This species was found only on O'ahu and has not been reported in more than a century (Berger 1981). It is considered to be extinct.

Bishop's 'O'o (Moho bishopi)

Despite intensive searches this species has not been recorded from Moloka'i since 1904 (Munro 1944; Pratt 1974; Scott, Woodside, and Casey 1977). The most recent searches in 1979 and 1980 failed to find it even on the remote Oloku'i Plateau (Scott et al., in press).

An unidentified black bird putatively regarded as Bishop's 'o'u has been reported from Maui (Sabo 1982). It remains to be determined if this represents a relict population of M. bishopi, some previously undescribed species, or a misidentified bird.

Hawai'i 'O'o (Moho nobilis)

There are no recent records for this species. It was not located during the HFBS (1976-1979), nor were any unidentified black birds reported during that survey (Scott et al., in press). "Black bird" sightings have been reported from Hawai'i, but none have the documentation needed to determine what species they represent (Banko and Banko 1980). If M. nobilis still exists on Hawai'i, the population must be small indeed (Scott et al., in press).

Kioea (Chaetophila angustipluma)

There are no records for kioea since the 19th century. It is widely considered to be extinct (Scott et al., in press).

'O'u (Psittirostra psittacea)

This species has become rarer in recent years on both Hawai'i and Kaua'i, the only 2 islands where it still occurs (Berger 1981). This is the only endangered passerine still found in Hawai'i Volcanoes National Park. The population on Hawai'i has been estimated to be 300 (Scott et al., in press). During the HFBS it was determined to be absent from many forests on Hawai'i where it was abundant at the turn of the century (Scott et al., in press). The low numbers and recent withdrawal from forests occupied in the 1940's and 50's (Richards and Baldwin 1953) do not bode well for its long-term survival. As with other Hawaiian species, avian malaria is thought to have played a major role in its decline. However, its low numbers and restricted distribution cannot be attributed to a single cause (Atkinson 1977; Scott et al., in press).

The Kaua'i population was estimated to be less than 10 birds in 1981 (Scott et al., in press), although this estimate may be low. There have been few recent records of 'o'u on Kaua'i. Like Kaua'i's other endangered forest birds, the 'o'u occurs in precariously low numbers.

Palila (Loxioides bailleui)

The palila is perhaps the best studied of the endangered Hawaiian passerines (van Riper 1978, 1980; van Riper, Scott, and Woodside 1978; Scott et al. 1984). The numbers of this species have varied from 1,600-6,400 birds since the first count in 1975. A major threat to its habitat was removed when most feral sheep were taken off Mauna Kea in 1982. Mouflon sheep pose an equally serious threat (Giffin 1983) and must be removed if the integrity of the palila's habitat is to be maintained. Introduced plants (particularly fountain grass Pennisetum setaceum and German ivy Senecio mikanioides) threaten to seriously modify the montane habitat of this species and increase the threat of fire (Berger et al. 1977; Scott et al. 1984).

Lesser Koa-finch (Rhodacanthis flaviceps)

One of the 6 large finch-billed species extant on the main islands when Cook discovered Hawai'i in 1778, the lesser koa-finch was known only from the koa forests of the upper leeward slopes of Mauna Loa (Munro 1944). There are no records of this species since Munro and Palmer collected their specimens in 1891, and it is undoubtedly extinct (Berger 1981; Scott et al., in press).

Greater Koa-finch (Rhodacanthis palmeri)

The largest of the historically known Hawaiian honeycreepers, the greater koa-finch sometimes flocked with the lesser koa-finch, and like the lesser fed extensively on the seeds of the koa tree as well as on other seeds and lepidopteran larvae (Perkins 1903).

Munro (1944) reported 2 unverified records of greater koa-finches that had been heard but not seen, one as late as 1937. We know of no other recent records and there appears to be little chance that this species survives on Hawai'i (Scott et al., in press).

Kona Grosbeak (Chloridops kona)

The Kona grosbeak, also known as the grosbeak finch, fed almost exclusively on hard naio seeds which its powerful jaws were well adapted to crack (Perkins 1903). This species has not been reported since the 1890's (Munro 1944), and it is doubtful that it still exists (Scott et al., in press).

Maui Parrotbill (Pseudonestor xanthophrys)

Maui parrotbills are found only in Maui's upper elevation forests, where they have been seen by almost every observer to visit their restricted range since this species was rediscovered in 1967 (Banko 1968; Scott and Sincock 1977). Subfossil remains have been found below 500 m on Maui and Moloka'i (S.L. Olson, pers. comm.). The species was widespread in prehistoric times; its present distribution is a small fraction of its former range. In the past its optimum habitat may well have been koa forests, most of which have been destroyed or severely degraded. Reforestation of upper montane koa-'ohi'a forest remnants would greatly enhance the survival chances of this species. The 1980 parrotbill population was estimated at 500 (Scott et al., in press). Almost the entire range of this species enjoys some form of legal protection. The principal threats are a severely truncated range at lower elevations, probably due to the occurrence of avian malaria, and the degradation of habitat by pigs, goats, and cattle. The browsing, grazing, and rooting activities of these animals are destroying native plants and accelerating erosion on the steep slopes of windward Haleakala.

Common 'Amakihi (*Hemignathus virens*)

This species is widespread and common on Maui, Hawai'i, and Kaua'i. It is rarer and its distribution more restricted on O'ahu and Moloka'i. It was last seen on Lana'i in 1977 (Hirai 1978) and is now believed to be extremely rare or extinct on that island. The population on Maui was recently estimated at 47,000, of which 3,000 were found on West Maui (Scott et al., in press). Lower densities were found in the drier forests on Maui than on Hawai'i.

On Hawai'i, where it is numerous, common 'amakihi are found as low as 300 m. In contrast to the situation on Maui, higher densities were found in drier forests at both high and low elevations. The population was estimated at 870,000 birds for the entire Island (Scott et al., in press).

The Moloka'i population of common 'amakihi has been estimated to be 1,800 birds. Interestingly, it is rare in the upper elevation native forests and common in the mixed native-exotic mesic forests below 1,000 m in the windward valleys (Scott, Woodside, and Casey 1977; Scott et al., in press). This is suggestive of a population resistant to whatever factors have eliminated native birds in extant lowland forests.

O'ahu has not been systematically surveyed like the other main islands. However, recent observations indicate that the common 'amakihi, while still uncommon there, is repopulating lowland areas (R.J. Shallenberger, pers. comm.).

Common 'amakihi, thought to number 2,300 in the Alaka'i Swamp in 1981 (Scott et al., in press), may have increased since the late 1960's (J.L. Sincock, unpubl. data). Common 'amakihi are very common in the koa and 'ohi'a forests of the Koke'e region, where they appear to thrive on the nectar of the introduced banana poka (*Passiflora mollissima*). The densities on Kaua'i were lower than those observed on either Maui or Hawai'i (Scott et al., in press).

'Anianiau (*Hemignathus parvus*)

This species is found only on Kaua'i, where it is widespread and common in the upper-elevation forests and, at least in the Alaka'i Swamp, appears to have not changed in abundance since the 1960's (Richardson and Bowles 1964; Scott et al., in press). 'Anianiau populations were estimated to be 5,500 in 1968-75 (J.L. Sincock, pers. comm.) and 6,000 in 1981. The entire Island population was estimated at 24,000 birds in the 1960's. This species appears to be in no danger of extinction.

Greater 'Amakihi (Hemignathus sagittirostris)

The greater 'amakihi was not observed during the intensive HFBS. It was last recorded in 1901 and is generally considered to be extinct (Berger 1981; Scott et al., in press).

Hawaiian 'Akialoa (Hemignathus obscurus)

This species was known from the islands of Hawai'i, Lana'i, and O'ahu. There are no recent records (Berger 1981). It was not found during the HFBS, and is probably extinct (Scott et al., in press).

Kaua'i 'Akialoa (Hemignathus procerus)

Rediscovered in 1960, the Kaua'i 'akialoa was considered rare at that time (Richardson and Bowles 1964). It was last reported in 1965 (Huber 1966), and was not seen by J.L. Sincock in his intensive searches of the forest, nor found by the observers during the 1981 HFBS (Scott et al., in press). The lack of sightings, as well as the failure of numerous other professional ornithologists to locate the bird during their visits to the Alaka'i Swamp (Sincock et al. 1984), suggest that this species must be rare if not extinct (Scott et al., in press).

Nukupu'u (Hemignathus lucidus)

This species has been found on Maui, O'ahu, and Kaua'i. It is considered extinct on O'ahu and is extremely rare on Kaua'i and Maui. J.L. Sincock saw only 2 birds during his 15 years of field work on Kaua'i. It was not found on Kaua'i during the 1981 HFBS. The Maui subspecies is very rare and has been reported less than 10 times since its rediscovery in 1967 (Banko 1968; Berger 1981). The population was estimated at 30 birds in 1980 (Scott et al., in press).

'Akiapola'au (Hemignathus munroi)

The 'akiapola'au is found only on the island of Hawai'i, where it was formerly widespread and abundant. It is now absent from lower elevation forests, is no longer found in the Kohala mountains, and is extremely rare in leeward forests. The present population has been estimated at 1,500 birds (Scott et al., in press). It is most frequently found in koa-'ohi'a forests where it is threatened by land-clearing as well as grazing and browsing by domestic cattle. The long-term chances of survival for this species and the syntopic 'akepa and Hawai'i creeper would be increased significantly by reforestation of high elevation pasturelands as well as protection and management of extant upland forests.

Kaua'i Creeper (Oreomystis bairdi)

This species was abundant in and near the Alaka'i Swamp in the 1960's (Richardson and Bowles 1964). The most recent survey of the Alaka'i Swamp, by HFBS 1981, indicated a population of 1,600 birds, which is not statistically different from the 2,300 birds estimated for this same area by J.L. Sincock (Scott et al., in press). During the HFBS we found the Kaua'i creeper rarer than both the common 'amakihi and the 'anianiau, whereas previously it was 2-3 times more common than these species. The Kaua'i creeper appears to be undergoing a decline in numbers and range even in the relatively undisturbed Alaka'i (Scott et al., in press).

Hawai'i Creeper (Oreomystis mana)

The status of this species has been clouded in the past by the inability of observers to accurately identify it (Scott, Conant, and Pratt 1979). Nevertheless, it is clear that the numbers and range of the Hawai'i creeper were reduced in the late 1930's and 1940's (Dunmire 1961). Today 98% of the 12,000 Hawai'i creepers estimated on Hawai'i are found in the Island's windward and Ka'u forests (Scott et al., in press). The biggest threats to the species' long-term survival are disease, logging, grazing, and urban development. Badly needed is the establishment and management of preserves in the upper montane koa-'ohi'a forests in which this and other endangered forest bird species are found, and reforestation of former 'ohi'a-koa forest now in pasture.

Maui Creeper (Paroreomyza montana)

This once-common species is no longer found on Lana'i (Munro 1944; Berger 1981), and was last reported in West Maui by Perkins (1903). In 1980 the population was estimated at 35,000 birds. Although it has a relatively large and dense population and has colonized in a forest of introduced species (Polipoli) over 15 km from the edge of its primary range, it has a sharply defined lower elevational limit at about 1,500 m over most of its range. In essence its large population masks a distribution similar to that of the crested honeycreeper and Maui parrotbill, suggesting that it is sensitive to the same constellation of stresses that has reduced populations of these endangered species.

Moloka'i Creeper (Paroreomyza flammea)

Despite intensive searches (Richardson 1949; Pratt 1974; Scott, Woodside, and Casey 1977; Scott et al., in press), this species has not been observed since the early 1960's (Pekelo 1963a, 1963b). Recent establishment of a Nature Conservancy preserve where this species was last recorded may enhance its chances of survival if it is still extant.

O'ahu Creeper (Paroreomyza maculata)

This species is considered to be rare on O'ahu (Shallenberger and Vaughn 1978; Berger 1981). As with the Hawai'i creeper, accuracy of field records has been a problem (Shallenberger and Pratt 1978), and its true status is not clear.

'Akepa (*Loxops coccineus*)

Originally, the 'akepa was known to occur on Hawai'i, Maui, O'ahu, and Kaua'i. It is considered extinct on O'ahu, although a bird recently reported with "all the markings of a female 'akepa" (Shallenberger and Vaughn 1978) may be indicative that it still exists there in very small numbers.

The Hawai'i population of this species has been estimated at 14,000, with 95% of these birds occurring in the windward forests of that island (Scott et al., in press). It has not been found in the Kohala mountains since the turn of the century (Berger 1981; van Riper 1982; Scott et al., in press). There have been few sightings in the last 40 years (Richards and Baldwin 1953; Casey 1973; Scott and Sincock 1977).

It has been estimated that fewer than 230 'akepa remain on Maui (Scott et al., in press), where the species has a fragmented distribution. As with the other rare species on Maui, the biggest threats to survival are avian diseases and habitat deterioration as the result of grazing and browsing by pigs and goats (Scott et al., in press).

The Kaua'i subspecies of 'akepa was estimated to number 1,700 birds in the Alaka'i Swamp in 1981 (Scott et al., in press). This is greater than the 600 birds estimated by Sincock for this same area during the period 1968-73. In addition, the 'akepa occurs in koa-'ohi'a forests adjacent to the Alaka'i Swamp, although a past estimate of population size indicated that 86% of the population occurs in the Alaka'i Swamp (J.L. Sincock, unpubl. data).

'Ula-'ai-hawane (*Ciridops anna*)

This species has not been observed since 1892 (Perkins 1903) and is widely considered to be extinct (Berger 1981; Scott et al., in press).

'I'iwi (*Vestiaria coccinea*)

This species was formerly abundant on all the main islands. It is now thought to be extinct on Lana'i (Hirai 1978), very rare on O'ahu (Shallenberger and Vaughn 1978), and to have a population of less than 100 birds on Moloka'i (Scott et al., in press).

The population of 'i'iwi on the island of Hawai'i was estimated at 340,000 birds (Scott et al., in press). It occurs in a wide variety of native forest types there but is very rare at lower elevations. This may be indicative of its susceptibility to avian diseases (van Riper et al., in press; Scott et al., in press). On Maui the 'i'iwi population was estimated at 19,000 birds in 1980, with 94% of these birds on East Maui. A localized population on West Maui has persisted within the same small area for many years (Scott et al., in press), suggesting a resident population.

In Kaua'i's Alaka'i Swamp the 'i'iwi population was estimated to be 5,000 in 1981. This is not statistically different from the 8,000 estimated for this same area by J.L. Sincock in 1968-75 (Scott et al., in press). 'I'iwi are commonly found in mixed native-exotic forests in the Koke'e region, where they feed extensively on the nectar of banana poka. Sincock has estimated that 70% of the population was found outside the Alaka'i during his studies.

Hawai'i Mamo (Drepanis pacifica)

This species has not been seen since 1898, and is considered to be extinct (Berger 1981; Scott et al., in press).

Black Mamo (Drepanis funerea)

The black mamo has not been reported since 1907 (Bryan 1908) despite extensive searches (Munro 1944; Richardson 1949; Pratt 1974; Scott, Woodside, and Casey 1977) and is considered to be extinct (Scott et al., in press).

Crested Honeycreeper (Palmeria dolei)

Although this species is extinct on Moloka'i and West Maui, a population of about 3,800 birds still resides in the upper elevation rain forests of windward Haleakala (Scott et al., in press). Although the crested honeycreeper is much more common than previously thought (Greenway 1958), it still faces problems. It occupies a relict range stressed by feral goats and pigs, and its range is abruptly truncated at lower elevations, suggesting that it is susceptible to introduced diseases. The establishment of The Nature Conservancy's Waikamoi Preserve should improve the long-term chances of survival for this species. The population will continue to be stressed until major portions of its essential habitat on State-owned land, east of the Preserve, are managed.

'Apapane (Himatione sanguinea)

The 'apapane was formerly abundant and widespread on all the main islands (Berger 1981). It remains abundant on Hawai'i and Maui, with 1 million and 110,000 birds, respectively (Scott et al., in press). There are about 39,000 'apapane on Moloka'i and 500 on Lana'i.

The Alaka'i Swamp population of 'apapane was estimated at 30,000 birds in 1981 (Scott et al., in press). This compares favorably with the 43,000 estimated for this same area in the late 1960's (J.L. Sincock, pers. comm.). The entire population of the Island was estimated at 163,000 in 1968-75 (J.L. Sincock, unpubl. data). Not only do 'apapane still occur in large numbers on most islands, but their occurrence down to 200 m elevation in some areas suggests that they are disease-resistant and gives occasion for optimism for this colorful member of an otherwise beleaguered group.

Po'ouli (Melamprosops phaesoma)

This recently discovered species is known only from the island of Maui (Casey and Jacobi 1974). A population of about 140 birds is restricted to an area of less than 2,000 ha in the upper-elevation 'ohi'a forest of windward Maui (Scott et al., in press). The po'ouli's very restricted distribution is but a fraction of its probable range prior to man's arrival (Olson and James 1982; Scott et al., in press), and it is severely stressed by feral pigs. Its survival into the 21st century may well depend upon the reduction or elimination of pigs within its highly relictual range.

CONSERVATION STATUS

Much effort has gone into preparing recovery plans for the birds of Hawai'i. Plans exist for all forest bird species on the islands of Hawai'i, Kaua'i, Maui, and Moloka'i. No plan exists for the O'ahu creeper or O'ahu 'akepa (table 1). Whereas many of the actions called for in those plans have been implemented, much remains to be accomplished. However, we believe that too often in Hawai'i, as elsewhere, we think only of what we have failed to accomplish rather than what we have done. We can point with pride to success stories by State agencies (e.g. removal of feral sheep and goats from Mauna Kea, establishment of Natural Area Reserves); private groups (establishment of 3 forest bird preserves and one seabird preserve); and Federal agencies (goat control program at Hawai'i Volcanoes National Park, initiation of introduced plant control programs, establishment of waterbird refuges by the FWS). The current public education efforts by Federal, State, and private groups are heartening.

However, we are at a crossroads in Hawai'i. Much more needs to be accomplished if we are to increase the chances of survival of Hawai'i's endemic avifauna. A solid information base exists on which to make sound management actions. Much has been done to legally protect endangered forest bird habitat, but critical gaps in protection exist, especially at upper elevations on

Table 1. Status of recovery plans for endangered and threatened land birds of the Hawaiian Islands.

Recovery Plan Title	Status	Species Covered
Nene	Approved 2/14/83	Nesochen sandvicensis
Hawaiian Hawk	Approved 5/9/84	Buteo solitarius
\`Alala (Hawaiian Crow)	Approved 10/28/82	Corvus hawaiiensis
Hawaiian Forest Birds	Approved 2/3/83	Psittirostra psittacea Hemignathus munroi Oreomystis mana Loxops coccineus coccineus
Palila	Approved 1/23/78	Loxioides bailleui
Kaua\`i Forest Birds	Approved 7/29/83	Phaeornis obscurus myadestina Phaeornis obscurus palmeri Moho braccatus Psittirostra psittacea Hemignathus procerus Hemignathus lucidus hanapepe

Recovery Plan Title	Status	Species Covered
Maui-Moloka'i Forest Birds	Approved 5/30/84	Phaeornis obscurus rutha Pseudonestor xanthophrys Hemignathus lucidus affinis Paroreomyza flammea Loxops coccineus ochraceus Palmeri dolei Melamprosops phaesoma
Leeward Islands	Approved May 1984	Telespyza cantans Telespyza ultima Acrocephalus f. familiaris Acrocephalus f. kingi

the island of Hawai'i, where native bird densities are greatest or could be expected to be high if perturbations by introduced species were removed. Legal protection is, however, only a first step (Kepler and Scott, in press). Also needed is vigorous implementation of management programs identified in recovery plans and elsewhere.

We believe that many of the major limiting factors for Hawai'i's native species have been identified. Some, such as avian malaria, while very important, have been shown to be geographically limited in their impact (van Riper et al. 1982). This makes design of preserves easier. Other limiting factors, such as browsing by feral ungulates (e.g. deer, cattle, goats, and pigs), are less restricted but may be easier to control. With the identification of major limiting factors has also come the identification of needed management actions.

The types of management that we feel must be implemented if we are to restore and maintain viable populations of Hawai'i's native birds are as follows:

1. Legal protection of natural habitats.
2. Elimination of introduced plants and animals in native habitats.
3. Physical restoration of native habitats through reforestation.
4. Intensive manipulation of birds in their natural habitats.
5. Translocation of endangered species into new, or improved former, habitats.
6. Captive propagation with release into the wild.

The 6 items are ranked in an order that we believe is indicative of our hope of successful use of management to protect or restore a species or community. Thus, for species with large populations and broad distributions that include low elevations and/or introduced vegetation (i.e. 'apapane, Hawaiian hawk), no specific actions need to be taken. The opposite extreme is represented by a species unable to survive in the wild without a continuing captive propagation effort (e.g. Hawaiian goose, Hawaiian crow). Many species in Hawai'i require several management actions simultaneously (table 2).

In a very real way, the position a species occupies on the list tells us where we are in our efforts to protect it. We have arrived with help "early" if we need only address item 1, and very late if we have to initiate captive propagation efforts.

Table 2. **Suggested** management actions needed to increase survival chances of Hawai`i's endangered land birds.

	Management Actions					
Species	Legal Protection of Natural Habitats	Elimination of Exotics	Physical Restoration of Habitats	Intensive Manipulation of Birds	Translocation of Endangered Species	Captive Propagation with Release
Hawaiian Goose		X		X		X
Hawaiian Hawk	X	X				
Hawaiian Crow	X	X	X	X	X	X
Hawaiian Thrush		X				
Small Kaua`i Thrush		X				X
Kaua`i `O`o		X				X
`O`u	X	X			X	X
Palila	X	X	X		X	
Maui Parrotbill	X	X	X			
Common `Amakihi (Moloka`i)		X			X	
Kaua`i `Akialoa		X				X
Nukupu`u		X				X
`Akiapola`au	X	X	X			

Table 2. Continued.

Species	Management Actions					
	Legal Protection of Natural Habitats	Elimination of Exotics	Physical Restoration of Habitats	Intensive Manipulation of Birds	Translocation of Endangered Species	Captive Propagation with Release
Hawai`i Creeper	X	X	X			
Moloka`i Creeper	X	X			X	X
O`ahu Creeper	X	X	X			
`Akepa	X	X	X			
Crested Honeycreeper	X	X	X		X	
Po`ouli		X				

While there have been many captive propagation efforts that have augmented wild populations, to our knowledge none of them, with the possible exception of the peregrine falcon effort, has yet successfully reestablished a naturally reproducing wild population (Fyfe 1977; Carpenter and Derrickson 1982; Carpenter 1983). Translocation efforts with wild birds or eggs have been more successful, and a number of species have been restored to former ranges and their numbers increased significantly with this technique. The trumpeter swan (Cygnus buccinator), bald eagle (Haliaeetus leucocephalus) and wild turkey (Meleagris gallopavo) rank among the success stories. Another species, the saddleback (Creadion carunculatus) of New Zealand, has been unequivocally saved by translocation from one island to another (Merton 1975).

Translocation and captive propagation require long, labor-intensive efforts focused on a single species. Furthermore, they require that land be legally protected, managed, and sometimes restored before reintroduction efforts can be initiated (see papers in Temple 1978 for examples of what has been done). Unfortunately in Hawai'i, many of the bird species are at the point where only clinical management (actions 4-6) will save them (table 2). However, in seeking to save what remains, we must not lose sight of what is possible. Heroic rescue operations such as required for the Hawaiian crow should not cause us to lose sight of the fact that restoration or protection and management of communities may result in far more species surviving for less money, and with far greater chances for success (Jacobi and Scott, this volume). We must try to anticipate future problems as well as deal with the present ones. Using the data presently available to us, we believe that we can take actions that will minimize the numbers of endangered species 100 years from now.

SPECIFIC MANAGEMENT RECOMMENDATIONS

We believe that sufficient information is available to make some specific management recommendations for Hawaiian birds. These are listed and discussed below.

Hawai'i

Hakalau Preserve. The upper elevation forests of windward Hawai'i harbor the core populations of the 'akiapola'au, Hawai'i creeper, and palila. Scientists and managers have identified this area as a potential forest bird preserve (Scott et al. 1983). The preserve would include relatively intact native forest as well as disturbed forest, which could be reforested. A major feature of the preserve would be 2 proposed corridors to link the koa-'ohi'a forests with the mamane forests of the Mauna Kea Game Management Area.

Ka'u-Kapapala corridor. The Kapapala Forest Reserve above about 1,500 m would serve to link Ka'u populations of endangered species with windward populations through Keauhou Ranch to Kilauea Forest Reserve. If established, this corridor would do much to increase the chances of survival of any endangered species that may repopulate the rapidly improving koa forests in the Mauna Loa strip of Hawai'i Volcanoes National Park.

Hualalai crow preserve. The Alala Recovery Plan calls for the establishment of a forest preserve of unspecified size on the northern slope of Hualalai. Small populations of 'akepa and Hawai'i creeper are known to occur in this area as well. We believe that the establishment of this preserve is crucial if the crow is to have any chance of survival.

Control of ungulates. Feral sheep, goats, and pigs, and feral and domestic cattle have caused serious damage to many of the plant communities in which endangered forest birds occur on Hawai'i. The numbers of these animals should be controlled in order to improve the habitat quality within the essential habitat of these birds. Emphasis should be placed on those areas above 1,500 m in elevation.

Banana poka. Banana poka poses a serious threat to the koa forest in the windward slopes of Mauna Kea and has recently spread to Volcano Village. It also is firmly established throughout northern Kona. These plants threaten the integrity of the native forests and should be controlled. USDA, NPS, and DLNR scientists are working toward this end by exploring many options, including biocontrol. These efforts deserve continued support.

Maui

Goats and pigs are serious threats to the integrity of the rain forests of Maui. Their activities have accelerated the erosion process on the steep slopes of Haleakala. Control of these animals should result in significant habitat improvement. Detailed plans for doing this are given in the Maui-Moloka'i Forest Bird Recovery Plan (Kepler et al. 1984).

The East Maui Irrigation Co. and State-owned land to the east of The Nature Conservancy's recently established Waikamoi Preserve are valuable habitat for no fewer than 5 species of endangered forest birds. This large area should be managed to protect the critical watersheds and the endangered species that reside there.

Axis deer. A population of the highly destructive Axis deer (*Axis axis*) is established on the low elevation slopes of west and south Haleakala. These animals should be eradicated before they become established in essential forest bird habitat on Haleakala's north or east slopes.

Moloka'i

Oloku'i. The magnificent Oloku'i is covered by pristine native forest, and the absence of ungulates is marked by a luxuriant carpet of native strubs, herbs, and bryophytes. In order to ensure the continuation of perhaps the only ungulate-free forest in Hawai'i, fencing is needed at the 600 m elevation level on the seaward ridge to it from Wailau Valley, to prevent pigs and axis deer from ascending the slopes.

Kamakou Preserve. The Nature Conservancy has acquired Kamakou Preserve on Moloka'i and has begun an ambitious management program. Lands adjacent to Kamakou should be similarly managed to protect the essential forest bird habitat that remains on East Moloka'i.

Kaho'olawe

This small island has no value for forest birds. Conservationists would be well advised to direct their efforts to preserve other more important areas in Hawai'i.

Kaua'i

The Alaka'i Swamp on Kaua'i has been dedicated as a Natural Area Reserve. If we are to maximize the chances of survival of the endangered species found there, we need to ensure that alien species are not introduced and that the numbers of pigs are reduced and goats eliminated from the area. In addition, we strongly recommend that alien species on the edge of the reserve (e.g. *Rubus argutus* and *Passiflora mollissima*) be controlled and that other alien plant species be prevented from becoming established.

In concluding, we wish to emphasize that many of the management actions we have recommended are dependent upon the cooperation of landowners. It is critical that we work with private, as well as public, landowners and consider their needs in attempts to maintain nearly native ecosystems. This strategy should reduce the chances for further extinctions and reduce the decline of common species to threatened or endangered status.

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LITERATURE CITED

Ashman, P.R., P. Pyle, and J. Jeffrey. 1984. A second nest of the small Kauai thrush. Elepaio 45:33-34.

Atkinson, I.A.E. 1977. A reassessment of factors, particularly Rattus rattus L., that influenced the decline of endemic forest birds in the Hawaiian Islands. Pac. Sci. 31(2):109-133.

Banko, P.C., and D.A. Manuwal. 1982. Life history, ecology, and management of nene (Branta sandvicensis) in Hawaii Volcanoes and Haleakala National Parks. Final Rep., Natl. Park Serv. Contract CX-8000-8-0005. Seattle: Univ. Wash. Coop. Natl. Park Resour. Stud. Unit.

Banko, W.E. 1968. Rediscovery of Maui nukupuu, Hemignathus lucidus affinis, and sighting of Maui parrotbill, Pseudonestor xanthophrys in Kipahulu Valley, Maui, Hawaii. Condor 70:265-266.

Banko, W.E. 1980-1983. History of endemic Hawaiian birds. Part 1. Population histories -- species accounts. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit, Avian Hist. Rep. 4-8. Honolulu: Univ. Hawaii.

Banko, W.E., and P.C. Banko. 1980. History of endemic Hawaiian birds. Part 1. Population histories -- species accounts: alala or Hawaiian raven/crow. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit, Avian Hist. Rep. 6b. Honolulu: Univ. Hawaii.

Berger, A.J. 1981. Hawaiian birdlife. 2nd ed. Honolulu: Univ. Pr. Hawaii.

Berger, A.J., E. Kosaka, J.M. Scott, P. Scowcroft, C. Wakida, D. Woodside, and C. van Riper, III. 1977. Palila recovery plan. U.S. Fish Wildl. Serv., Portland, Ore.

Bryan, W.A. 1908. Some birds of Molokai. B.P. Bishop Mus. Occ. Pap. 4:133-176.

Burr, T., P.Q. Tomich, E. Kosaka, W. Kramer, J.M. Scott, E. Kridler, J. Giffin, D. Woodside, and R. Bachman. 1982. Alala recovery plan. U.S. Fish Wildl. Serv., Portland, Ore.

Carpenter, J.W. 1983. Species decline: a perspective on extinction recovery and propagation. Zoo Biol. 2:165-178.

Carpenter, J.W., and S.D. Derrickson. 1982. The role of captive propagation in preserving endangered species. In Nongame and endangered wildlife symposium, ed. R.R. Odum. Georgia Dep. Nat. Res. and Georgia Chapt. Wildl. Soc.

Casey, T.L.C. 1973. Preliminary report on the birdlife in Waihoi Valley, Maui. Elepaio 34:46-50.

Casey, T.L.C., and J.D. Jacobi. 1974. A new genus and species from the island of Maui, Hawaii (Passeriformes: Drepanididae). B.P. Bishop Mus. Occ. Pap. 24(12):215-226.

Devick, W.S. 1981a. Status of the nene population on the island of Hawaii between 1975 and 1980. Hawaii Dep. Land Nat. Resour., Honolulu. Typescript.

Devick, W.W. 1981b. Status of the nene population on the island of Maui between 1975 and 1980. Hawaii Dep. Land Nat. Resour., Honolulu. Typescript.

Dunmire, W.W. 1961. Birds of the national parks in Hawaii. Honolulu: Hawaii Nat. Hist. Assn.

Fyfe, R.W. 1977. Reintroducing endangered birds to the wild. In Endangered birds: management techniques for preserving threatened species, ed. S.A. Temple, 323-329. Madison, Wis.: Univ. Wisconsin Pr.

Giffin, J.G. 1982. Ecology of the mouflon sheep on Mauna Kea. Final Rep., Hawaii Dep. Land Nat. Resour. Pittman-Robertson Proj. W-17-R, Stud. R-3.

Giffin, J.G. 1983. Alala investigations. Final Rep., Hawaii Dep. Land Nat. Resour. Pittman-Robertson Proj. W-18-R, Stud. R-II-B (1976-1981).

Greenway, J.C., Jr. 1958. Extinct and vanishing birds of the world. Am. Comm. Internatl. Wildl. Protect. Spec. Pub. 13. New York.

Henshaw, H.W. 1902. Birds of the Hawaiian Islands, being a complete list of the birds of the Hawaiian possessions with notes on their habits. In Hawaiian Almanac and Annual for 1902, 54-106. Honolulu: Thos. G. Thrum.

Hirai, L.T. 1978. Native birds of Lanai, Hawaii. West. Birds 9:71-77.

Howarth, F.G. Impacts of alien land arthropods and mollusks on native plants and animals in Hawaii. [This volume]

Huber, L.N. 1966. Field notes. Alakai Swamp, Kauai; March 1965. Observations of akialoa. Elepaio 26:71.

Jacobi, J.D., and J.M. Scott. An assessment of the current status of native upland habitats and associated endangered species on the island of Hawaii. [This volume]

Kear, J., and A.J. Berger. 1980. The Hawaiian goose: an experiment in conservation. Vermillion, S. Dakota: Buteo Books.

Kepler, C.B., and A.K. Kepler. 1983. A first record of the nest and chicks of the small Kauai thrush. Condor 85:497-499.

Kepler, C.B., T.A. Burr, C.B. Cooper, D. Dunatchik, J. Medeiros, J.M. Scott, M. Ueoka, and W. Wong. 1984. Maui-Molokai forest bird recovery plan. U.S. Fish Wildl. Serv., Portland, Ore.

Kepler, C.B., and J.M. Scott. In press. Conservation of island ecosystems. In Proc. 18th World Conf. Internatl. Counc. Bird Preserv. Cambridge, England.

Kirch, P.V. 1982. The impact of the prehistoric Polynesians on the Hawaiian ecosystem. Pac. Sci. 36:1-14.

Merton, D. 1975. The saddleback: its status and conservation. In Breeding endangered species in captivity, ed. R.D. Martin, 61-74. New York: Academic Pr.

Mountainspring, S., and J.M. Scott. In press. Interspecific competition among Hawaiian forest birds. Ecol. Monogr.

Munro, G.C. 1944. Birds of Hawaii. Honolulu: Tongg Pub. Co.

Olson, S.L., and H.F. James. 1982. Fossil birds from the Hawaiian Islands: evidence for wholesale extinction by man before Western contact. Science 217(4560):633-635.

Pekelo, N., Jr. 1963a. Some notes from Molokai. Elepaio 23:64.

Pekelo, N., Jr. 1963b. Some notes from Molokai. Elepaio 24:17-18.

Perkins, R.C.L. 1903. Vertebrata. In Fauna Hawaiiensis, ed. D. Sharp, Vol. 1, Pt. IV, 365-466. Cambridge, England: The Univ. Pr.

Pratt, H.D. 1980. Intra-island variation in the elepaio on the island of Hawaii. Condor 82: 449-458.

Pratt, T. 1974. Plant communities and bird distribution in east Molokai. Elepaio 33:66-70.

Richards, L.P., and P.H. Baldwin. 1953. Recent records of some Hawaiian honeycreepers. Condor 55: 221-222.

Richardson, F. 1949. Status of native land birds of Molokai. Pac. Sci. 3:226-230.

Richardson, F., and J. Bowles. 1964. A survey of the birds of Kauai, Hawaii. B.P. Bishop Mus. Bull. 227.

Sabo, S.R. 1982. The rediscovery of Bishop's 'o'o on Maui. Elepaio 42:69-70.

Scott, J.M., J.K. Baker, A.J. Berger, E. Kosaka, L. Landgraf, C.J. Ralph, D. Woodside, R. Bachman, and T. Burr. 1983. Hawaii forest bird recovery plan. U.S. Fish Wildl. Serv., Portland, Ore.

Scott, J.M., S. Conant, and H.D. Pratt. 1979. Field identification of the Hawaiian creeper on the island of Hawaii. West. Birds 10:71-80.

Scott, J.M., S. Mountainspring, F.L. Ramsey, and C.B. Kepler. In press. Forest bird communities of the Hawaiian Islands: their dynamics, ecology, and conservation. Stud. Avian Biol.

Scott, J.M., S. Mountainspring, C. van Riper III, C.B. Kepler, J.D. Jacobi, T.A. Burr, and J.G. Giffin. 1984. Annual variation in the distribution, abundance and habitat of the palila. Auk 101:647-664.

Scott, J.M., and J.L. Sincock. 1977. Recent observations on the birds of the Koolau Forest Reserve, Maui. West. Birds 8:113-116.

Scott, J.M., D.H. Woodside, and T.L.C. Casey. 1977. Observations of birds in the Molokai Forest Reserve, July 1975. Elepaio 38:25-27.

Scowcroft, P.G., and J.G. Giffin. 1983. Feral herbivores suppress mamane and other browse species on Mauna Kea, Hawaii. J. Range Manage. 36:638-645.

Scowcroft, P.G., and H.F. Sakai. 1983. Impact of feral herbivores on mamane forests of Mauna Kea, Hawaii: bark stripping and diameter class structure. J. Range Manage. 36:495-498.

Shallenberger, R.J., and H.D. Pratt. 1978. Recent observations and field identifications of the Oahu creeper. Elepaio 38:135-140.

Shallenberger, R.J., and G.K. Vaughn. 1978. Avifaunal survey in the central Koolau range, Oahu. Honolulu: Ahuimanu Prod.

Sincock, J.L., R.E. Daehler, T. Telfer, and D.H. Woodside. 1984. Kauai forest bird recovery plan. U.S. Fish Wildl. Serv., Portland, Ore.

Smith, J.D. 1952. The Hawaiian Goose (nene) restoration program. J. Wildl. Manage. 16:1-9.

Smith, C.W. Impact of alien plants on Hawaii's native biota. [This volume]

Stone, C.P. Alien animals in Hawaii's native ecosystems: toward controlling adverse effects of introduced vertebrates. [This volume]

Stone, C.P., R.L. Walker, J.M. Scott, and P.C. Banko. 1983. Hawaiian goose management and research -- where do we go from here? Elepaio 44:11-15.

Temple, S.A. 1978. Endangered birds: management techniques for preserving threatened species. Madison, Wis.: Univ. Wisconsin Pr.

U.S. Fish and Wildlife Service. 1983. Republication of lists of endangered and threatened species. Fed. Register 50 CFR 17.11 and 17.12.

van Riper, C., III. 1978. The breeding biology of the amakihi (*Loxops virens*) and palila (*Psittirostra bailleui*) on Mauna Kea, Hawaii. Ph.D. Diss., Univ. Hawaii, Honolulu.

van Riper, C., III. 1980. Observations on the breeding of the palila (*Psittirostra bailleui*) of Hawaii. Ibis 122:462-475.

van Riper, C., III. 1982. Censuses and breeding observations of the birds on Kohala Mountain, Hawaii. Wilson Bull. 94:463-476.

van Riper, C., III, and J.M. Scott. 1979. Observations on distribution, diet and breeding of the Hawaiian thrush. Condor 81:65-71.

van Riper, S., and C. van Riper III. A summary of known parasites and diseases recorded from the avifauna of the Hawaiian Islands. [This volume]

van Riper, C., III, J.M. Scott, and D. Woodside. 1978. Distribution and abundance patterns of the palila on Mauna Kea, Hawaii. Auk 95:518-527.

van Riper, C., III, S.G. van Riper, M.L. Goff, and M. Laird. 1982. The impact of malaria on birds in Hawaii Volcanoes National Park. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. 47. Honolulu: Univ. Hawaii.

van Riper, C., III, S.G. van Riper, M.L. Goff, and M. Laird. In press. The epizootiology and ecological significance of malaria in Hawaiian landbirds. Ecology.

Warner, R.E. 1968. The role of introduced diseases in the extinction of the endemic avifauna. Condor 70:101-120.

Warshauer, F.R., J.D. Jacobi, A. LaRosa, J.M. Scott, and C.W. Smith. 1983. The distribution, impact and potential management of the introduced vine Passiflora mollissima (Passifloraceae) in Hawaii. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. 48. Honolulu: Univ. Hawaii.

4.

CONSERVATION STATUS OF NATIVE TERRESTRIAL INVERTEBRATES IN HAWAI'I

Wayne C. Gagne and Carl C. Christensen

ABSTRACT

The native invertebrate fauna of the Hawaiian Islands consists of some 6,000 arthropod species, 1,000 or more native land mollusks, and an undetermined number of taxa belonging to other phyla. Many elements of this fauna are restricted to narrow geographical or ecological limits. Because the evolution of the fauna took place in a high degree of geographical isolation, its members are unusually vulnerable to novel selection pressures resulting from the introduction and spread of non-native animal and plant species and from ecological disturbance caused by human activities. A great many native invertebrates have become extinct since initial human settlement of these islands, and many other species are now in imminent danger of extinction. Nevertheless, many native invertebrates survive in locations where the native vegetation is relatively pristine or where other favorable conditions are present. Efforts to conserve native invertebrates are hindered by inadequacies of available taxonomic and ecological data and by the low priority usually accorded to invertebrates by those agencies charged with protection of the native biota. Efforts to protect native invertebrates are of 3 types: taxon-specific protection under Federal and State Endangered Species Acts; site-specific actions providing protection to habitat necessary to the survival of native invertebrates; and preventive or eradicative actions targeting undesirable alien species. Although all extant species of _Achatinella_ (a genus of tree snails endemic to O'ahu) have been listed as "endangered" by the U.S. Department of the Interior (USDI), no other Hawaiian invertebrates have yet received such legal protection. A preliminary conservation assessment has been made for about 800 species of insects, providing a cross-section of ecological functional groups, i.e., aquatic and semiaquatic (Odonata: 28 species of _Megalagrion_), anthophagous and cleptoparasitic (Hymenoptera: 63

species of *Nesoprosopis*), phytophagous (Lepidoptera: 22 species of *Hedylepta*), and detritivorous (Coleoptera: 140 species of Nitidulidae; Diptera: 500 species of Drosophilidae). Based on this and other information, more than 300 native arthropods have been identified by the USDI as candidates for possible designation as threatened or endangered species. The International Union for the Conservation of Nature and Natural Resources has identified a number of additional invertebrate taxa as endangered or threatened. The National Park Service, The Nature Conservancy of Hawai'i, and the State of Hawai'i provide important protection for habitat necessary for the survival of native invertebrates, although management of lands under State jurisdiction often subordinates wildlife preservation to competing land uses. Restrictions on the importation of alien animal and plant species and the control of established pest species are also important to the conservation of Hawaiian invertebrates. Much additional research is needed to provide data on the biology of Hawaiian invertebrates, to identify taxa at risk of extinction, and to aid in the design and management of natural reserves providing protection to these animals.

INTRODUCTION

An assessment of the conservation status of native Hawaiian terrestrial invertebrates must concern itself with more than 6,000 arthropods, some 1,000 native land snail species, and an unknown number of representatives of various less prominent phyla. Basic taxonomic data are unavailable for many of these species, and significant ecological information has been obtained for only a few of the insects and almost none of the land mollusks. The great diversity, taxonomic uncertainty, and ecological ignorance make any assessment of the conservation status of these animals a formidable, indeed almost impossible, task. As specifics are unavailable, conservationists working with Hawaiian invertebrates have of necessity dealt in generalities; the comparative wealth of species and dearth of data have led them to group ecologically related rather than taxonomically related species into "guilds" or ecological functional groups (e.g., Gagne 1979), or to declare whole genera as endangered (e.g., *Achatinella* tree snails) or threatened (e.g., picture-winged *Drosophila* pomace flies). Nevertheless, some ecological constants influence invertebrates in much the same way as they do better-known groups of organisms. Like vertebrate and plant species, invertebrates have certain basic needs for survival:

1. A sufficient amount of the particular habitat to which each species is adapted.
2. The presence of adequate numbers of individuals of other species to which each is reproductively and

ecologically linked.

3. A sufficiently large extant population that the probability of extinction is minimized (Simberloff 1983).

Where data are available, these commonalities permit the conservation needs of invertebrate taxa to be treated in much the same way as those of other taxa.

ENDEMICITY AND VULNERABILITY

Among terrestrial macroinvertebrates, arthropods and mollusks are the most frequent colonizers of tropical oceanic islands. Other groups are only sporadically successful in long-distance over-water dispersal. Even so, successful natural colonizations of the Hawaiian Islands by macroinvertebrates were infrequent. The 6,000+ species of Hawaiian terrestrial arthropods are derived from about 300-400 successful colonization events; similarly, the approximately 1,000 species of native land mollusks are derived from about 22-24 colonizations (Zimmerman 1948). The ability of terrestrial invertebrate colonizers to speciate extensively on tropical oceanic islands is well known. In Hawai'i it is exemplified in the explosive radiations of drosophilid pomace flies (the 800+ endemic Hawaiian species, of a worldwide fauna of 2,500 species, are descended from 1-2 colonizing immigrant species) and amastrid and endodontid land snails (the almost 300 species of the endemic family Amastridae and approximately 200 Hawaiian Endodontidae are apparently each derived from single colonization events). At least a half-dozen insect genera each include more than 100 endemic species. In some instances, members of these radiations have diversified over a relatively short time to fill a broad range of ecological niches, which in continental ecosystems are usually occupied by totally unrelated taxa having a long evolutionary history of adaptation to those niches.

The interplay of isolating mechanisms (geographical, behavioral, ecological, etc.) has resulted in the high degree of localized endemicity and/or narrow niche specialization characteristic of terrestrial invertebrates in Hawai'i. Although no overall assessment has been made, we estimate that the vast majority of our terrestrial insect species are single-island endemics, and that the same holds true for nearly all of the larger land mollusks and many of the minute species. For example, 87% of the 100+ species of picture-winged Drosophila are restricted to single islands, and 9 of the 13 species inhabiting 2 or more islands are shared by Maui and Moloka'i, islands which were joined with Lana'i and Kaho'olawe to form a single island (termed "Maui Nui" by geologists) in periods of low sea level during the Pleistocene. Characteristically, these flies are found in higher altitude rain forests from 300 to 2,000 m, where they breed on various native plant materials. Like many of the host plants that support them, the fly populations are patchy in distribution. Their population sizes are comparatively small, and most of the species are narrowly host-specific. Similarly, no species of the large achatinelline tree snails (genera Achatinella, Partulina, Perdicella, and Newcombia) is known to occur on more than one island, and populations are often highly localized within islands.

The native Hawaiian invertebrate fauna is unusual in that many ecological niches are occupied by taxa which have only recently evolved the major adaptations necessary to exploit their particular niches. It includes a large number of endemic species, most of them narrowly precinctive in either ecological or geographical terms, or both. Much more than in continental ecosystems, the diversity of Hawaiian invertebrates arose in place from the adaptive radiation of a few progenitor species. The coevolution of native invertebrates and other endemic plant and animal taxa took place in association with a different suite of predators and competitors than those present in continental areas.

The unusual nature of the Hawaiian invertebrate fauna contributes to the vulnerability of its members when their habitats are suddenly altered by human activity; or when habitats are altered by introduction of new predators or competitors, or even other species on which predators or competitors are dependent (Wells, Pyle, and Collins 1983). Invertebrate taxa with restricted geographical ranges are highly susceptible to extinction as a result of habitat destruction caused by human activities. Polynesian and modern commerce has vastly increased the pace of immigration by plant and animal species and of the ecological changes resulting from the establishment of these novel competitors and/or predators. Native species able to adapt to naturally occurring change taking place on a geological or evolutionary time scale are overwhelmed by a multitude of new influences acting simultaneously or in close sequence. The large monophyletic adaptive radiations characteristic of the Hawaiian land snail fauna may be particularly subject to mass extinction, as large numbers of taxa over a wide area may be similarly vulnerable to novel threats. Examples are the hypothesized catastrophic impact of predation by ants on eggs and juveniles of endodontid land snails (Solem 1976) and predation on achatinellid and other snails by the introduced predatory snail Euglandina rosea (Wells, Pyle, and Collins 1983).

PERTURBATIONS AND EXTINCTIONS

It is clear that the Hawaiian invertebrate fauna has suffered widespread recent extinctions, but documenting the extent and chronology of those extinctions is a difficult task. To a considerable extent, this is because of our incomplete knowledge of the true diversity of the pristine biota. Ornithologists have only recently learned of an unsuspected diversity of the native avifauna of the Hawaiian Islands through study of fossils and subfossils from limestone sinkholes and lava tubes (Olson and James 1982a, 1982b). Entomologists who wish to estimate the original diversity of the Hawaiian arthropod fauna and the extent of recent extinctions are frustrated by an absence of fossil data, although hopes remain that such evidence will eventually be recovered. Malacologists have long been aware of the occurrence of fossil land snails in areas now devoid of these animals (Henshaw 1904; Perkins 1913; Zimmerman 1948) and might be expected to have a rather clear understanding of the extent of molluscan extinctions. Unfortunately, this is not the case, as until very recently studies of fossil land mollusks were strictly taxonomic in focus, while detailed information on the recent status of the living fauna was restricted to the large and colorful _Achatinella_ tree snails of O'ahu; even here, post-World War II data are limited. For minute species or for larger species inhabiting islands other than O'ahu, available data are generally few and out of date. Kondo (1970) has estimated that about 50% of the native land snail taxa originally inhabiting the Hawaiian Islands is extinct. In the absence of more precise data, his analysis stands as a first approximation.

It should be remembered, however, that biologists, paleontologists, and archaeologists have only recently begun to study prehistoric and protohistoric extinction phenomena in Hawai'i. Furthermore, it is difficult to distinguish extinction events that may have occurred in the hundreds of years before European rediscovery of these islands, from those that took place in the 50-75 years following Captain Cook's landing and preceding the mid-19th century observations of knowledgeable local naturalists.

Despite the lack of hard data regarding invertebrate extinctions, we shall attempt to summarize their recent history. It is a history dominated by the effects of anthropogenic habitat destruction and the introduction and spread of alien plants and animals. Although human impact is evident throughout, no single agent is influential in all cases; rather, multiple agents acting sequentially or simultaneously have combined to cause catastrophic extinctions.

The Pristine Environment

Prior to the entry of man into the Hawaiian environment, change occurred in geological or evolutionary time scales. Geological events such as erosion, volcanic eruptions, and sea level changes had an influence, but at a pace and on a scale to which native invertebrates could adapt. Coevolution of native plants and animals was also a gradual process, with successful new immigrants reaching the Hawaiian Archipelago every few thousand years or so (inter-island colonizations would of course have been a more frequent occurrence). Such newly arrived colonists must have occasionally adversely affected established residents, but in general the native Hawaiian biota evolved in relative isolation from the outside world. While occasional extinction would of course have been a part of the evolutionary process, catastrophic extinction not restricted to localized geographical areas or to particular evolutionary lineages was probably infrequent.

Prior to human settlement, no significant fossil evidence is available for the native arthropod fauna, and direct evidence of its original diversity is limited, particularly for the lowland areas which have now been most heavily impacted by man. It is logical to assume, however, that these areas once supported numerous now-extinct endemic forms. Studies of relictual faunas on Nihoa Island (Conant et al. 1984) and possibly on certain offshore islands adjacent to the inhabited main islands (see Hobdy 1982 for botanical data from such locations) may yield valuable information on the native arthropods formerly inhabiting lowland regions. Upland areas are less heavily modified, and a greater portion of their arthropod faunas survives.

Fossil evidence from numerous sites in the lowlands of the main Hawaiian Islands provides considerable information regarding the now-extirpated native land snail faunas formerly inhabiting these areas. Fossil deposits in the coastal lowlands of Kaua'i contain representatives of a diverse native mollusk fauna which included a dozen or more now-extinct species of the amastrid genus Carelia (Hawai'i's largest native land snails, some with shells 85 mm in length), as well as other amastrids and numerous helicinid, endodontid, and ground-dwelling achatinellid snails. In windward O'ahu, the arboreal Achatinella may be found in coastal fossil deposits at Kahuku, La'ie, Kailua, and Waimanalo, along with many other native snails. On Moloka'i, tree snails of the genera Partulina and Newcombia are common fossils in coastal dunes at Mo'omomi. Arid leeward regions such as Barbers Point and Diamond Head on O'ahu, western Kaua'i, Ni'ihau, and Kaho'olawe, were inhabited by distinctive assemblages of xerophilous ground-dwelling snails.

Dextral pupillid snails of the genus Lyropupa were abundant in such sites, as were certain amastrids, succineids, and other taxa adapted to arid conditions. Upland dry forests, as in Kohala and Kona on the island of Hawai'i (Christensen 1983; Christensen 1984b) also supported diverse assemblages of land snails. Moist upland habitats contained diverse land snail faunas, and various native achatinellids (e.g., Achatinella, Partulina, Auriculella, Tornatellides), succineids (Succinea, Catinella) and helicarionids (Philonesia) may still be locally abundant in suitable locations. The original diversity of this zone is unknown, however, since such ground-dwelling taxa as the Amastridae and Endodontidae are probably under-represented in the modern fauna as a result of recent extinctions. Accurate knowledge of the diversity of this zone must await studies of fossils from sediments in lava tubes.

Prehistoric Human Impacts

The colonizing Polynesians converted much of the lowlands to agricultural uses or to anthropogenic grasslands (Kirch 1982). Destruction of the native lowland vegetation could only have had a catastrophic effect on the invertebrate fauna dependent on that vegetation. Direct evidence of extinction of invertebrates during this period is becoming available as a result of interdisciplinary studies of fossil land snails from archaeological sites. Kirch (1975) used such data to demonstrate deforestation in Halawa Valley, Moloka'i. In studies of sediments from limestone sinkholes at Barbers Point, O'ahu, Christensen and Kirch (in prep.) and their associates at Bishop Museum are finding a consistent pattern of extirpation of native amastrid and endodontid snails, probably occurring during the prehistoric period. Land clearance by the Polynesians no doubt also had a devastating effect upon native arthropods.

The immigrant Polynesians brought a number of plant and animal species with them. Many of the 2 dozen or so plant species they introduced were highly domesticated or infertile cultivars with little tendency to invade undisturbed environments, although such species as kukui (Aleurites moluccana), ti (Cordyline terminalis), and a few others became naturalized members of otherwise native communities (see Wagner, Herbst, and Yee, this volume). The impact of predation by introduced gekkonid and scincid lizards is impossible to assess. Of the 4 bird and mammal species introduced prehistorically (the domestic chicken, dog, and pig, and the Polynesian rat Rattus exulans), the last is likely to have had the greatest impact on native invertebrates due to predation on ground-dwelling insects and snails. Although feral pigs (Sus scrofa) now cause massive destruction to vegetation in native habitats, it is possible that this may be a recent phenomenon (Stone, this volume). The Polynesians did introduce a few invertebrates (including the land snails Lamellaxis gracilis and Lamellidea oblonga, possibly the cockroach Allacta similis, and several arthropod ectoparasites of vertebrates), but these are not presently known to have had major impacts on native invertebrates.

Historic Impacts

Many of the adverse effects of man's direct and indirect impacts on native Hawaiian ecosystems are not specific to invertebrates and will be discussed by other participants in this Symposium. The advent of the historic period saw an increase in the pace of habitat destruction as a direct result of man's activities, as well as an increase in the rate of introduction of alien plants and animals.

Zimmerman (1948) discussed the effects of introduced ants (particularly the big-headed ant Pheidole megacephala) on native insects, and Solem (1976) suggested that predation by ants has been catastrophic for endodontid snails, a particularly vulnerable group. Although some 200 species of Hawaiian endodontids are represented in Bishop Museum collections, mostly from fossil sites, we know of less than a half-dozen occasions in which living endodontids have been encountered in the main Hawaiian Islands within the last 40 years. Probably best-documented is the continuing decrease in the abundance and range of O'ahu's Achatinella tree snails (Hart 1975, 1978; U.S. Fish and Wildlife Service 1980; Hadfield, in press). Here habitat degradation and destruction resulting from land clearance, fire, the activities of alien ungulates, and the spread of alien plants have combined with the effects of predation by rats (Atkinson 1977), shell collectors, and the snail Euglandina rosea (Hadfield and Mountain 1981) to cause the extinction of 50% or more of the 41 recognized species. The introduction of Euglandina as part of a biocontrol program targeted at the giant African snail Achatina fulica was particularly unfortunate; malacologists have long warned of the hazards to native land mollusks inherent in the introduction of such predators (Mead 1956; van der Schalie 1969). Ironically, although biocontrol advocates have introduced Euglandina to numerous Pacific islands over the last 30 years (Mead 1979), they have not yet demonstrated this predator to exercise effective control over the giant African snail (Christensen 1984a). Claims have been made that Euglandina has not been a major factor in recent extinctions of Achatinella and other native land snails, but demonstration of the devastating impact of this species on partulid tree snails in French Polynesia (Tillier and Clarke 1983; Clarke, Murray, and

Johnson 1984) should remove any doubts regarding its influence in Hawai'i. Oxychilus alliarius, an alien snail that became established in Hawai'i in the 1930's, may also prey on native land mollusks (Severns 1984). Although Hyman (1939) regarded the terrestrial flatworm Geoplana septemlineata as a Hawaiian endemic, we suggest that it is not native here and may have had a severe impact on ground-dwelling snails. Parasitism by the nematode Angiostrongylus cantonensis may also be harmful to native land mollusks. If so, this would be an indirect effect of the introduction of Achatina fulica, as this species is one of the principal intermediate hosts of this parasite and may have been the vehicle for its establishment in Hawai'i (Alicata 1966).

The effects of rat predation on invertebrates have been studied in Australia and New Zealand (Best 1969; Gales 1982), where a number of rodent-free offshore islands harbor large, flightless insects that are nearly extirpated on the New Zealand mainland and other offshore islands, where they are recorded only as subfossils or as relicts in restricted favorable locations in these areas (Key 1978; Ramsay 1978; Foggo and Meurk 1981). In Hawai'i, apparently ratless Nihoa Island provides a close parallel, as large flightless crickets and earwigs exist there but are unknown in the main islands (Conant et al. 1984). Nihoa also has numerous species which represent native groups now extirpated from lowlands on the main islands. In Hawai'i, National Park Service workers have recently embarked on studies of rodent impacts on native insects and other animals, which should provide additional information in this regard (Loope and Stone 1984; Stone et al. 1984). Predation or parasitism by other introduced animals adversely affects many other native invertebrates as well, and indirect effects due to destruction of host plants necessary to the survival of particular invertebrate species may also be important; for example, 9 species of pyralid moths (genus Hedylepta) have become extinct since 1900 as a result of biocontrol introductions or because of loss of host plants (Gagne and Howarth, in press). Additional examples could be provided (Howarth 1983a), but those listed are sufficient to outline the dimensions of the problem.

CURRENT DISTRIBUTION AND DIVERSITY OF NATIVE INVERTEBRATES

The classic work of Swezey (1954) provided much data about the occurrence of Hawaiian insects. More recently, Gagne (1979, 1980, 1981) has provided an assessment of the pattern of diversity among native arthropods in Hawaiian ecosystems based on an extrapolation of his sampling of Acacia koa and Metrosideros polymorpha canopies along an altitudinal transect from sea level to tree line in Hawai'i Volcanoes National Park from 1971 to 1973. From this data base, obtained as part of the Island Ecosystems Subprogram of the International Biological Program (IBP), he derived measures of species diversity, biomass, and richness. It was found that the mid-elevation closed-canopy rain forest (Zone D and the lower portion of Zone E of Ripperton and Hosaka 1942) scored highest for these measures, with lesser values at higher and lower elevations. The low diversity found at high elevations was thought due to low temperature, low relative humidity, and low harvestable productivity in open canopy forests subject to grazing by introduced ungulates. Predation by introduced temperate insects preadapted to cooler elevations might also be a factor. The low diversity of native insects at lower elevations correlated with increasing prevalence of predatory ants which, in conjunction with alien cockroaches, comprised most of the insect biomass. For islands not attaining elevations as great as those of Hawai'i and Maui, the less diverse, high-elevation zone would not be represented, and the general pattern would be one of increasing native arthropod diversity with increasing altitude.

The limited nature of recent field observations of native land snail faunas makes an analysis of their current distribution difficult. Given our current state of ignorance, no species-by-species or habitat-by-habitat analysis is possible, and the following remarks are intended to provide a highly simplified overview of the status of major genera.

In general, areas of disturbed vegetation at elevations below about 300 m are inhabited by land mollusk faunas dominated by introduced snails and slugs. Native taxa are limited to a few hardy succineids (Succinea), minute ground-dwelling achatinellids (Lamellidea, Tornatellides), and an occasional pupillid (Lyropupa, subgenus Mirapupa). The diverse assemblages of native amastrids, endodontids, and other snails that formerly occupied such sites have been extirpated. Mid-elevation disturbed forests may contain the same few minute achatinellids and the pupillid Pronesopupa, but alien taxa predominate. Significant numbers of native taxa are rarely encountered below about 300 m elevation, their abundance increasing at higher elevations in moist regions of relatively undisturbed native vegetation. Here achatinelline tree snails (Achatinella, Partulina) and other Achatinellidae (Auriculella and several genera of minute snails) may still be found in favored localities, as may succineids (Succinea, Catinella), helicarionids (Philonesia), occasional amastrids (Leptachatina, more rarely Amastra), and an infrequent helicinid (Pleuropoma). Few native snails are likely to be found in drier areas where native understory vegetation has been replaced by introduced grasses. Alien slugs and snails have invaded most habitats, even in some locations where native plant species predominate, and the predatory snails Euglandina rosea and Oxychilus alliarius are widespread in such localities (the former species occurring to elevations of 1,000 m or more in places, the latter occurring abundantly to elevations in excess of 2,000 m). Although field data are very few, land snail diversity at high elevations (> 2,200 m) is low and was probably never high.

CONSERVATION STATUS AND STRATEGIES

Actions by governmental and other agencies to protect native invertebrates are of 3 main types: taxon-specific protection under the Federal Endangered Species Act or state equivalents; site-specific actions that protect the habitats of native invertebrates (as well as other native wildlife); and preventive or corrective actions targeting undesirable alien species.

Taxon-Specific Actions

Official recognition of threatened or endangered status for native invertebrates has been slow in coming, compared to that for vertebrates. Local specialists recognize large numbers of invertebrate species which merit official recognition. As with the native avifauna and flora, a large percentage of native arthropods appear to have become extinct recently, and many of the survivors should be considered candidates for endangered or threatened species categorization. The situation confronting large-sized terrestrial mollusks is even more grim, for if present trends continue many will probably be extirpated over much of their already greatly reduced range, largely as a result of predation by the introduced snail Euglandina rosea (U.S. Fish and Wildlife Service 1980; Hadfield and Mountain 1981). Most native invertebrates will not soon gain legal recognition without changes in political and public attitudes about the importance of invertebrates in human welfare and natural ecosystem functioning, and without funding for efforts to determine the conservation status of taxa. A trend that should accelerate this process has been to designate as endangered species whole genera or portions of them with similar ecologies or behavior. A recent example is Federal recognition of the endangered status of all extant species (approximately 19 in number) of O'ahu tree snails of the genus Achatinella.

Gagne (1982) has made a preliminary conservation assessment of about 800 native terrestrial arthropod species. These species provided a cross-section of ecological functional groups as follows: 28 aquatic, semi-aquatic, and terrestrial narrow-winged damselflies of the genus Megalagrion (Odonata, Coenagrionidae); 60 anthophagous and cleptoparasitic bee species of the genus Nesoprosopis (Hymenoptera, Hylaeidae); 22 species of moths in the genus Hedylepta (Lepidoptera, Pyralidae); 140 species of detritivorous and nectarivorous nitidulid souring beetles of various genera (Coleoptera); and 550 species of detritivorous and predaceous pomace flies in the genera Drosophila, Titanochaeta, and Scaptomyza (Diptera, Drosophilidae). From the outset of the project, the problem was how best to determine "endangered," "threatened," and "common" ranking in a manner that would give a uniform basis for assessing the conservation status of each species. A numerical scoring system called the "Index of Rarity" was developed, with values for taxonomic understanding, biological uniqueness, and impacts. According to this ranking, a priority for Federal review could be assigned following the U.S. Fish and Wildlife Service criteria for consideration of listing species as endangered or threatened (these criteria are reviewed by Wagner, Herbst, and Yee, this volume). The ideal situation would be a detailed biological and systematic study of each species following bibliographic and collection analysis. Even though the "Index of Rarity" method is fraught with pitfalls, some elements of this system have been adopted by the Office of Endangered Species for application nationally (G. Drewry, pers. comm.). The arthropod species were arrayed against island, general habitat type, the protection (or lack) afforded by existing reserves, etc., to attempt a systems approach to their conservation and protection.

Based on data from this and other sources, the U.S. Fish and Wildlife Service has identified 335 species of native Hawaiian invertebrates as candidates for possible inclusion on the List of Endangered and Threatened Wildlife (U.S. Fish and Wildlife Service 1984). The bulk of these are "Category 2" taxa, for which available information indicates listing as endangered or threatened is possibly appropriate, but for which biological data on vulnerability and threats are as yet insufficient to justify listing. No Hawaiian invertebrates were identified as "Category 1" taxa, those for which currently available data support the appropriateness of proposals for listing. No Hawaiian insects have yet been listed, although insects comprise the great majority of the recently identified animal candidate species. Two Kaua'i cave invertebrates, the no-eyed big-eyed spider Adelocosa anops and the Kaua'i cave sandhopper Spelaeorchestia koloana, were once under consideration for recognition, but with the seemingly interminable changes of criteria for completing the review procedures necessary for listing, their processing has lapsed and needs to be re-initiated. Future lists of candidate taxa should include additional native arthropods, as well as a much-expanded selection of terrestrial mollusks. (The amastrid genus Carelia, the only Hawaiian mollusks on the recent list of candidates, was assigned to "Category 3A," taxa believed to be extinct.)

Hawai'i has a State Endangered Species Act to determine the conservation status of endemic invertebrates, but so far responsible State agencies have taken little initiative other than to follow Federal determinations. This inaction on the local scene reflects a general lack of awareness or concern by governmental officials and the general public, about the unique nature of the Hawaiian biota (particularly its terrestrial ecosystems) and its vulnerability to disturbance. A concerted effort to instill a conservation ethic needs to be directed at all educational levels.

At the international level, the International Union for the Conservation of Nature and Natural Resources (IUCN) publishes the Red Data Books that indicate the global conservation status of plant and animal species as endangered, threatened, vulnerable, commercially threatened, etc. The Invertebrate Red Data Book (Wells, Pyle, and Collins 1983) lists the ca. 100 species of Hawaiian picture-winged Drosophila as vulnerable, and the 19 or so extant Achatinella tree snails and the no-eyed big-eyed spider as endangered. The IUCN is considering the once widespread narrow-winged damselfly, Megalagrion pacificum (Moore and Gagne 1982), for endangered status.

Site-Specific Actions

Federal lands under the jurisdiction of the National Park Service (Hawai'i Volcanoes National Park, Haleakala National Park) and U.S. Fish and Wildlife Service (Northwestern Hawaiian Islands National Wildlife Refuge, particularly Nihoa and Necker Islands) contain important habitat for native invertebrates and receive considerable protection from activities unfavorable to their continued survival. The full protective provisions of the Federal Endangered Species Act are applicable to other federally owned land in Hawai'i. At the State level, the Natural Area Reserve System provides protection to some habitats vital to native invertebrates, but additional reserves need to be designated, and management efforts within existing reserves need to be increased. With regard to State regulation of designated Conservation District lands, preservation of native wildlife habitat is often accorded a low priority when conflicts arise with such competing land uses as hunting, commercial forestry, and energy development. One non-governmental agency, The

Nature Conservancy of Hawai'i, has become active in the preservation of natural areas and has initiated a State Natural Heritage Program to more accurately pinpoint areas needing protection (Holt and Fox, this volume). In addition to those invertebrates recognized as threatened or endangered by international, Federal, and State levels, species which are recognized by local authorities as being *de facto* endangered or threatened (whether this arises from systematic analysis of published data or merely from a "best-guess" assessment) are considered in the setting of priorities for preservation of natural areas.

Restrictions on Importation of Alien Organisms

Many of the problems confronting native invertebrates stem from the introduction of alien plant and animal species that may compete with, prey on, parasitize, or otherwise adversely affect native invertebrates or their host plants (see Howarth this volume). A first step in reducing such impacts should be a strengthening of quarantine and inspection regulations for materials shipped to Hawai'i from outside the State. Candidate biocontrol agents should be subjected to careful environmental review prior to release. The demise of native moth species of the genus *Hedylepta* and of various tree snails points out the hazards sometimes associated with such well-intended introductions.

Selection and Design of Natural Preserves

Natural preserve selection and design are topics of considerable current research and debate (see bibliographies by Harty, Harnish, and Lehman 1981; Killian 1982; Pearsall 1983; and Franklin, this volume). Most studies address preserve design requirements of vertebrates, especially birds, and to a lesser extent of plants; a number debate the applicability or limitations of island biogeographic theory to conservation practices. Few studies deal with habitat design for invertebrates. Despite the limited consideration given invertebrates in these studies, natural habitat preserve design that contains sound scientific reasoning should have applicability to all native biota. A suitable approach may be to join elements of a systems approach which combine the identification of critical area conservation (which delineates most threatened insular ecosystems) with endangered species determination (see Jacobi and Scott, this volume). Both efforts, when combined and when based on sound scientific data, could be productive conservation measures (see Eckhardt 1983). For now, conservationists concerned with Hawaiian invertebrates will have to be content with preserve selection and conservation programs that are tailored to birds and showy flowering plants, biotic elements that are better-known scientifically and that more easily gain the attention of the public.

Fortunately, almost any native habitat in some semblance of its original condition will contain many invertebrate species, and some Hawaiian invertebrates such as the Achatinella tree snails have gained a certain degree of public recognition in their own right. Invertebrate zoologists should, however, urge the protection of certain unique ecosystems that do not harbor endangered vertebrates but which are of sufficient importance to justify particular efforts on their behalf based solely on the presence of rare invertebrates or diversity of taxa. The recently discovered aeolian ecosystems atop Hawai'i's highest mountains are worthy of protection, as are lava caves inhabited by endangered invertebrates. These latter sites are the subject of study by the Cave Species Specialist Group of the IUCN's Species Survival Commission; investigations will include terrestrial invertebrates in cave ecosystem conservation (Howarth 1983b). Small islands offshore from the main Hawaiian Islands are likely to harbor relict populations of native invertebrates, as well as of endangered flowering plants.

Research Needs

As the foregoing discussion has demonstrated, our understanding of the conservation status and management needs of native Hawaiian invertebrates is deficient in a number of areas. Excluding general topics not specifically related to invertebrates, we believe the most important research tasks to be undertaken are as follows:

1. Completion of conservation assessment of selected terrestrial arthropods (particularly candidate endangered and threatened species), including analyses of both field and archival data.

2. Identification of additional candidate endangered and threatened species among native terrestrial mollusks. Achatinelline tree snails of the genera Achatinella, Partulina, Newcombia, and Perdicella should be given priority consideration because distributional data are relatively good; the extreme vulnerability of endodontid land snails recommends them also for consideration.

3. Biosystematic and ecological study of those high ranking species determined by available criteria to be most vulnerable to extinction.

4. Development of methods to eliminate or ameliorate influences (habitat destruction, spread of introduced organisms, etc.) that increase the vulnerability of native invertebrates to extinction.

5. Determination of the extent of suitable habitat necessary to support populations of particular vulnerable taxa and, if possible, the population size necessary to ensure their continued survival.

6. Design, delineation, and management of natural reserves to provide protection to native invertebrates

in conjunction with conservation needs of other biotic elements.

Though gathering this much information for a significant portion of Hawai'i's diverse invertebrate fauna is a tall order, a similar effort has already been completed for 6 species of endangered Mainland butterflies (Arnold 1983a, 1983b), and it is possible to do the same for any of our species or species groups given the necessary commitment of resources. What we learn about each species will speed--but not obviate--research on the remainder (Simberloff 1983).

CONCLUSIONS

We hope we have not painted too discouraging a picture of the conservation outlook for native invertebrates in Hawai'i. Although much has already been lost, recent discoveries of invertebrates living in previously unknown cave and high-altitude ecosystems and of such unexpected creatures as the predatory geometrid caterpillar Eupithecia demonstrate that the natural environment of Hawai'i still includes a diverse assemblage of native invertebrates. We disagree emphatically with those who say that it is already too late to salvage a significant fraction of that assemblage. One conclusion that is clear to any student of Hawaiian invertebrates is the need to educate the general public, and those in positions to influence land-use and conservation planning, about the uniqueness and diversity of this important element of the Hawaiian biota. We hope that future conservation efforts in Hawai'i will accord invertebrates an appropriate place alongside the vertebrate and plant taxa that are the usual focus of such efforts.

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LITERATURE CITED

Alicata, J.E. 1966. The presence of Angiostrongylus cantonensis in islands of the Indian Ocean and probable role of the giant African snail, Achatina fulica, in dispersal of the parasite to the Pacific Islands. Can. J. Zool. 44:1041-1049.

Arnold, R.A. 1983a. Ecological studies of six endangered butterflies (Lepidoptera, Lycaenidae): island biogeography, patch dynamics, and the design of habitat preserves. Univ. Calif. Pub. Entomol. 99.

Arnold, R.A. 1983b. Conservation and management of the endangered Smith's blue butterfly, Euphilotes enoptes smithi (Lepidoptera: Lycaenidae). J. Res. Lepidoptera 22(2):135-153.

Atkinson, I.A.E. 1977. A reassessment of factors, particularly Rattus rattus L., that influenced the decline of endemic forest birds in the Hawaiian Islands. Pac. Sci. 31(2):109-133.

Best, L.W. 1969. Food of the roof-rat, Rattus rattus rattus (L.), in two forest areas of New Zealand. New Zealand J. Sci. 12:258-267.

Christensen, C.C. 1983. Analysis of land snails. In Archaeological investigations of the Mudlane-Waimea- Kawaihae road corridor, island of Hawaii: an interdisciplinary study of an environmental transect, ed. J.T. Clark and P.V. Kirch, 449-471. B.P. Bishop Mus. Dep. Anthropol. Rep. Ser. 83-1.

Christensen, C.C. 1984a. Are Euglandina and Gonaxis effective agents for biological control of the giant African snail in Hawaii? [Abstract] Am. Malacol. Bull. 2:98-99.

Christensen, C.C. 1984b. Analysis of nonmarine mollusks. In Subsistence and conflict in Kona, Hawaii: an archaeological study of the Kuakini Highway realignment corridor, ed. A.R. Schilt, 355-376. B.P. Bishop Mus. Dep. Anthropol. Rep. Ser. 84-1.

Christensen, C.C., and P.V. Kirch. In prep. Nonmarine mollusks and ecological change at Barbers Point, Oahu, Hawaii. B.P. Bishop Mus.

Clarke, B.C., J. Murray, and M.S. Johnson. 1984. Extinction of endemic species by a program of biological control. Pac. Sci. 38(2):97-104.

Conant, S., C.C. Christensen, P. Conant, W.C. Gagne, and M.L. Goff. 1984. The unique terrestrial biota of the Northwestern Hawaiian Islands. Proc. 2nd Symp. Resour. Invest. Northwest. Hawaii. Islands, May 25-27, 1983. Vol. 1, 77-94.

Eckhardt, J.P. 1983. The Conservancy's endangered species program. Nat. Conservancy News 33(6): 14-17.

Foggo, M.N., and C.D. Meurk. 1981. Notes on a visit to Jacquemart Island in the Campbell Island Group. New Zealand J. Ecol. 4:29-31.

Franklin, J.F. Design of natural area preserves in Hawaii. [This volume]

Gagne, W.C. 1979. Canopy-associated arthropods in Acacia koa and Metrosideros tree communities along an altitudinal transect on Hawaii Island. Pac. Insects 21(1):56-82.

Gagne, W.C. 1980. Altitudinal distribution and composition of arthropods in ohia (Metrosideros collina subsp. polymorpha) canopies in the Hawaii Volcanoes National Park with ecological implications for some native biota. Proc. 3rd Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 115-123. Honolulu: Univ. Hawaii.

Gagne, W.C. 1981. Altitudinal distribution of organisms along an island mountain transect: canopy-associated arthropods. In Island ecosystems: biological organization in selected Hawaiian communities, ed. D. Mueller-Dombois, K.W. Bridges, and H.L. Carson. Stroudsburg, Penn.: Hutchinson Ross Pub. Co.

Gagne, W.C. 1982. Working toward an assessment of the conservation status of Hawaii's endemic arthropods, with emphasis on the moths or Lepidoptera. Proc. 4th Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 63-72. Honolulu: Univ. Hawaii.

Gagne, W.C., and F. G. Howarth. In press. Conservation status of endemic Hawaiian Lepidoptera. Proc. 2nd Europ. Lepidopt. Congr., ed. J. Heath.

Gales, R.P. 1982. Age- and sex-related differences in diet selection by Rattus rattus on Stewart Island, New Zealand. New Zealand J. Zool. 9:463-466.

Hadfield, M.G. In press. Extinction in Hawaiian achatinelline snails. Malacologia.

Hadfield, M.G., and B.S. Mountain. 1981. A field study of a vanishing species, *Achatinella mustelina* (Gastropoda, Pulmonata), in the Waianae Mountains of Oahu. *Pac. Sci.* 34(4):345-358.

Hart, A.D. 1975. Living jewels imperiled: collectors, introduced pests and trees decimate land snails. *Defenders* 50(6):482-486.

Hart, A.D. 1978. The onslaught against Hawaii's tree snails. *Nat. Hist.* 87(10):46-57.

Harty, F.M., C.L. Harnish, and G.M. Lehman. 1981. A partial bibliography of recent literature relevant to the design and management of nature reserves. *J. Nat. Areas Assn.* 1(2):11-12.

Henshaw, H.W. 1904. On certain deposits of semi-fossil shells in Hamakua District, Hawaii, with descriptions of new species. *J. Malacol.* 2:56-64.

Hobdy, R. 1982. A vegetative survey of Maui County's offshore islets. *Proc. 4th Hawaii Volcanoes Natl. Park Nat. Sci. Conf.*, 87-92. Honolulu: Univ. Hawaii.

Holt, R.A., and B. Fox. Protection status of the native Hawaiian biota. [This volume]

Howarth, F.G. 1983a. Classical biocontrol: panacea or Pandora's box. *Proc. Hawaii. Entomol. Soc.* 24 (2&3):239-244.

Howarth, F.G. 1983b. The conservation of cave invertebrates. *Proc. 1st Internatl. Cave Manage. Symp., Murray, Ky. July 15-18, 1981*, 57-64.

Howarth, F.G. Impacts of alien land arthropods and mollusks on native plants and animals in Hawaii. [This volume]

Hyman, L.H. 1939. Land planarians of the Hawaiian Islands. *Arch. Zool. Exp. Gen.* 80:116-124.

Jacobi, J.J., and J.M. Scott. An assessment of the current status of native upland habitats and associated endangered species on the island of Hawaii. [This volume]

Key, K.H.L. 1978. *The conservation status of Australia's insect fauna*. Australian Natl. Parks Wildl. Serv. Occ. Pap. 1.

Killian, R. 1982. Selected natural diversity bibliography with annotations. Nat. Areas J. 2(4):12-27.

Kirch, P.V. 1975. Excavations at Sites A1-3 and A1-4: early settlement and ecology in Halawa Valley. In Prehistory and ecology in a Windward Hawaiian valley: Halawa Valley, Molokai, ed. P.V. Kirch and M. Kelly, 17-70. Pac. Anthropol. Rec. 24.

Kirch, P.V. 1982. The impact of the prehistoric Polynesians on the Hawaiian ecosystem. Pac. Sci. 36:1-14.

Kondo, Y. 1970. Colloquium on endangered species of Hawaii: extinct land molluscan species. B.P. Bishop Mus., Honolulu. Typescript.

Loope, L.L., and C.P. Stone. 1984. Introduced vs. native species in Hawaii. A search for solutions to problems of island biosphere reserves. Proc. 1st Internatl. Congr. Biosphere Reserves, 252-257.

Mead, A.R. 1956. Predators need defending. Nautilus 70(2):65-69.

Mead, A.R. 1979. Economic malacology with particular reference to Achatina fulica. In The Pulmonates, vol. 2B, ed. V. Fretter and J. Peake, 1-150. London: Academic Pr.

Moore, N.W., and W.C. Gagne. 1982. Megalagrion pacificum (McLachlan)--a preliminary study of the conservation requirements of an endangered species. Rep. Odon. Spec. Group 3. Gland, Switzerland: Internatl. Union Conserv. Nat. and Nat. Resour.

Olson, S.L., and H.F. James. 1982a. Fossil birds from the Hawaiian Islands: evidence for wholesale extinction by man before Western contact. Science 217(4560):633-635.

Olson, S.L., and H.F. James. 1982b. Prodromus of the fossil avifauna of the Hawaiian Islands. Smithson. Contrib. Zool. 365.

Pearsall, S. 1983. Additions to diversity bibliography. Nat. Areas J. 3(3):3-6.

Perkins, R.C.L. 1913. Introduction. In Fauna Hawaiiensis, ed. D. Sharp, Vol. 1, xv-ccxxviii, pls. 1-16. Cambridge, England: The Univ. Pr.

Ramsay, G.W. 1978. A review of the effect of rodents on the New Zealand invertebrate fauna. In The ecology and control of rodents in New Zealand nature reserves, ed. P.R. Dingall, I.A.E. Atkinson, and C. Hay, 89-97. Wellington: New Zealand Dep. Lands Surv.

Ripperton, J.C., and E.Y. Hosaka. 1942. Vegetation zones of Hawaii. Hawaii Agric. Exp. Stn. Bull. 89.

Severns, M. 1984. Another threat to Hawaii's endemics. Hawaii. Shell News 32(12):1, 9.

Simberloff, D. 1983. What a species needs to survive. Nat. Conservancy News 33(6):18-22.

Solem, A. 1976. Endodontoid land snails from Pacific Islands (Mollusca: Pulmonata: Sigmurethra). Part I: Family Endodontidae. Chicago: Field Mus. Nat. Hist.

Stone, C.P. Alien animals in Hawaii's native ecosystems: toward controlling the adverse effects of introduced vertebrates. [This volume]

Stone, C.P., P.C. Banko, P.K. Higashino, and F.G. Howarth. 1984. Interrelationships of alien and native plants and animals in Kipahulu Valley, Haleakala National Park: a preliminary report. Proc. 5th Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 91-105. Honolulu: Univ. Hawaii.

Swezey, O.H. 1954. Forest entomology in Hawaii: an annotated check-list of the insect faunas of the various components of the Hawaiian forests. B.P. Bishop Mus. Spec. Pub. 44.

Tillier, S., and B.C. Clarke. 1983. Lutte biologique et destruction du patrimoine genetique: le cas des mollusques gasteropodes pulmones dans les territoires francais du Pacifique. Genet. Sel. Evol. 15(4):559-566.

U.S. Fish and Wildlife Service. 1980. Endangered and threatened wildlife and plants; proposed endangered status for Achatinella, a genus of Hawaiian tree snails. Fed. Register 45(125): 43358-43360.

U.S. Fish and Wildlife Service. 1984. Endangered and threatened wildlife and plants; review of invertebrate wildlife for listing as endangered or threatened species. Fed. Register 49(100): 21664-21675.

van der Schalie, H. 1969. Man meddles with nature--Hawaiian style. The Biologist 51(4): 136-146.

Wagner, W.L., D.R. Herbst, and R.S.N. Yee. Status of the native flowering plants of the the Hawaiian Islands. [This volume]

Wells, S.M., R.M. Pyle, and N.M. Collins, comps. 1983. The IUCN Invertebrate Red Data Book. Gland, Switzerland: Internatl. Union Conserv. Nat. and Nat. Resour.

Zimmerman, E.C. 1948. Insects of Hawaii. Vol. 1, Introduction. Honolulu: Univ. Hawaii Pr.

5.

PROTECTION STATUS OF THE NATIVE HAWAIIAN BIOTA

R. Alan Holt and Barrie Fox

ABSTRACT

For purposes of assessing the level of protection currently enjoyed by the native Hawaiian biota, a definition for "protected natural areas" is presented. A "protected natural area" is an area where affirmative legal action is required to allow serious disturbance by man thereon, and where active management to control non-native processes, species, and ecosystems is under way. Using this definition, public and private lands designated for management to conserve the native biota are listed and their protected status assessed. Of the 23% of the State's lands so listed, most fail to fully meet the definition of "protected natural areas." Any assessment of how well the present natural area system represents the range of native habitat types and endangered species, is seriously impaired by 1) lack of a definitive classification of Hawaiian ecosystems, and 2) lack of a single, comprehensive repository of rare species information. It is clear, however, that several important habitat types are not included in any currently protected natural area, and that most endangered plant species are also excluded. Recommendations for an improved system of protected natural areas include 1) establishment of an ongoing data base to determine protection needs; 2) support of effective management of existing protected areas; 3) provision for legal protection of naturally protected (by isolation or rugged terrain) areas; 4) protection of additional properly designed areas; 5) improvement of credibility of native species conservation.

INTRODUCTION

Over 415,000 ha in Hawai'i (23% of the State) are included in lands legally dedicated to the conservation of native species and ecosystems. All of these lands--National Park Service lands, U.S. Fish and Wildlife Service National Wildlife Refuges, State of Hawaii

Sanctuaries and Natural Area Reserves (NAR's), The Nature Conservancy preserves, and State of Hawai'i Protected Conservation Subzones--have been set aside by people with the idea that they will form a legacy, an ark to carry the important functions, products, and aesthetics of native Hawaiian species and ecosystems into the future for the benefit of our descendants. In this paper we try to answer 2 questions related to the goal of perpetuating the native biota. First, how well does our present system of protected natural areas protect the Hawaiian biota? Second, what should we do next?

DEFINING "PROTECTION"

What do we expect from a so-called "protected natural area"? We establish it with the intent that it will carry functioning native ecosystems or populations of unique plants and animals into the future. To protect a natural area for this purpose we must make 2 kinds of commitments.

First, we must commit ourselves and others <u>not</u> to do certain things on these lands. We must agree not to clear forests for residential or agricultural development, not to build an industrial facility there, not to allow any human activity that will adversely change the natural conditions that exist. This is largely a legal or political commitment.

Second, and perhaps less obvious, we must commit ourselves to actively <u>do</u> certain things. This is a commitment of funds and manpower to mitigate those threats to the native ecosystem that have already been or may in the future be introduced, and which, if left untended, will seriously degrade the natural values which the area was established to protect. Before we can expect an area to maintain its diversity and stability by its own natural processes, we must commit ourselves to actively protect those processes from radical disruption by introduced organisms such as feral pigs (<u>Sus scrofa</u>), goats (<u>Capra hircus</u>), and weeds, and from destabilizing abiotic processes such as fire and rapid erosion (often promoted by introduced organisms). With the exception of a very few isolated mountain tops, offshore islets, and lava tubes, the typical Hawaiian natural area today would suffer dramatically from disruption by alien species if we simply put a fence around it and left it alone.

For the purposes of this paper, a "protected natural area" may be defined as an area of land where 1) an affirmative legal action would be required to allow human activities to occur which would seriously disturb the native ecosystem, processes, or species thereon;

and 2) where an active management program is under way to control non-native biotic and resultant abiotic disruption of the native ecosystem, processes, and species thereon.

PROTECTED AREAS IN HAWAI'I

How the conservation of "protected" lands in Hawai'i meets this definition of a protected natural area is shown in table 1. Not included are small privately protected areas. Also excluded are State and county parks, portions of forest reserves not in Subzone "P", and National Historic Parks where the chief management mandate is for recreation, forest products development, or anything other than native biota conservation; the important contributions of these areas to species and ecosystem protection are discussed later in this paper.

Of the 48 areas listed, 20 presently have both legal protection and active threat control programs. Five of these are large ecosystem preserves. Fifteen are areas dedicated to a relatively few rare species, generally birds or rare plants.

Areas where no affirmative legal action would be required to remove their protected status are those under short-term leases, cooperative agreements or permits. In each of these cases, the administering authority has decided that the benefits to ecosystems or important components thereof justify less-than-binding legal protection, often because more binding legal protection is simply not available or affordable. These areas are either small or are sites for limited management of a relatively few rare species (e.g., Hawaiian goose (Nesochen sandvicensis) sanctuaries, waterbird refuges, seabird nesting sites). The single area with neither legal nor active threat protection (Paradise Pacifica waterbird habitat) is similar in nature.

Sixteen of the natural areas in table 1 have legal protection but no active program for control of non-native threats. These include all 13 State NAR's (totalling 32,830 ha), all "Protected" Conservation Subzone lands (236,340 ha), the State Alaka'i Wilderness Preserve (4,020 ha) and The Nature Conservancy's Hakalau Preserve (1,330 ha). All are large ecosystem preserves, together accounting for 237,700 ha or 57% of all protected land in the State.

ECOSYSTEM PROTECTION

In addition to creating adequately protected natural areas, our goal must be to develop a system of areas which protects the fullest possible array of the

Table 1. Protected status of Hawaiian natural areas, by agency.

Natural Areas	Area (ha)	Legal Protection*	Active Threat Control Program*
<u>Federal</u>			
National Park Service			
HALE NP (Maui)	11,678	Yes	Yes
HAVO NP (Hawai\`i)	92,784	Yes	Yes
	104,425		
U.S. Fish and Wildlife Service Refuges			
Pearl Harbor NWR (O\`ahu)	25	No	Yes
James Campbell NWR (O\`ahu)	57	No	Yes
Kakahai\`a NWR (Moloka\`i)	17	Yes	Yes
Hanalei NWR (Kaua\`i)	371	Yes	Yes
Hule\`ia NWR (Kaua\`i)	96	Yes	Yes
Kilauea Pt. WAS (Kaua\`i)	13	No	Yes
Hawaiian Islands NWR	708	Yes	Yes
	1,287		
U.S. Department of Defense			
Nu\`upia Ponds (O\`ahu)	205	No	Yes
Ulupa\`u Head (O\`ahu)	13	No	Yes
Naval Ammunition Depot (O\`ahu)	36	No	Yes
	254		
Subtotal for Federal Natural Areas	105,966		

Natural Areas	Area (ha)	Legal Protection*	Active Threat Control Program*
<u>State</u>			
NAR's (13 areas)	32,826	Yes	No
"P" Subzone	236,345	Yes	No
Alaka`i Wilderness Preserve (Kaua`i)	4,022	Yes	No

	273,193		
Sanctuaries (Animal or Aquatic)			
Hawai`i State Seabird Sanctuary (Offshore Islets)	121	Yes	Yes
Paiko Lagoon (O`ahu)	13	Yes	Yes
Kanaha Pond (Maui)	58	Yes	Yes
Kipuka `Ainahou (Hawai`i)	15,540	Yes	Yes
Kahuku (Hawai`i)	8,094	No	Yes
Keauhou I (Hawai`i)	3,278	No	Yes
Keauhou II (Hawai`i)	4,047	No	Yes
Paradise Pacifica (Kaua`i)	4	No	No
Mana Ponds (Kaua`i)	3	No	Yes

	31,158		
Sanctuaries (Primarily Plant)			
Gardenia (O`ahu)	< 0.1	Yes	Yes**
Manawainui Gulch (Maui)	23	Yes	Yes**
Polipoli *Geranium* (Maui)	0.6	Yes	Yes**
Koai`a (Hawai`i)	5	Yes	Yes**
Pu`uwa`awa`a *Hibiscadelphis* (Hawai`i)	< 0.1	Yes	Yes**
Mauna Kea Silversword (Hawai`i)	20	Yes	Yes**
Powerline Road Silversword (Hawai`i)	0.3	Yes	Yes**
Sesbania arborea (Moloka`i)	4	Yes	Yes**

	53		

Table 1. Continued.

Natural Areas	Area (ha)	Legal Protection*	Active Threat Control Program*
Subtotal for State Natural Areas	337,371		
Private			
The Nature Conservancy			
Hakalau (Hawai`i)	1,335	Yes	No
Kipahulu (Maui)	397	Yes	Yes
Kamakou (Moloka`i)	1,123	Yes	Yes
Waikamoi (Maui)	2,117	Yes	Yes
Kaluahonu (Kaua`i)	88	No	Yes
Subtotal for Private Areas	5,060		
Total	415,430		

* As defined in text.

** Fencing only.

remaining Hawaiian biota. We should try to include in our natural areas the best remaining examples of all native ecosystems and species. In Hawai'i, with highly localized endemism, we must include natural areas from all the islands in order to capture a full representation of the flora and fauna.

Assessing our progress thus far in ecosystem protection is difficult because many protected areas have not been inventoried even at the ecosystem level. This is especially true of State lands. A major obstacle to completing such a basic inventory is that we do not have a definitive classification of terrestrial Hawaiian ecosystems. That is, we lack a standard vocabulary for concisely describing what one person may call "mixed mesophytic forest" and what someone else may call "dryland forest" from the exact same site. This lack of standard language makes it difficult to get the ecosystem information that does exist into an interpretable form.

Wayne Gagne and James Jacobi are both working on classification systems for Hawaiian ecosystems. In the meantime, we can use the vegetation zones developed by Ripperton and Hosaka (1942) and modified by Gagne and Mueller-Dombois (n.d.) to chart the general vegetation types included in protected natural areas (table 2). The numbers in the table are the numbers of protected areas on a given island of a given vegetation type. The number to the left of the slash is the number of fully (legally *and* biologically) protected areas, and the number to the right of the slash is the number of partially (legally *or* biologically) protected areas. State plant sanctuaries and "P" Subzone lands are not included. Most of Ripperton and Hosaka's vegetation types actually include several major ecosystem types. For example, #7 Aquatic Zone includes wetlands, streams, anchialine pools, marine pools, and lakes.

Listing the protected natural areas in this way reveals several important shortcomings in coverage of geographical and ecological areas for protection. All of the vegetation zones are included in the system, but the islands of Ni'ihau, Lana'i, and Kaho'olawe are totally excluded. The only natural areas on O'ahu with active threat control programs are waterbird wetlands. On Kaua'i and O'ahu, the wetland is the only vegetation zone that has both legal protection and active threat control. There is no actively managed example of the habitat types richest in rare plant species--mixed mesophytic forest on Kaua'i and O'ahu and lowland rain forest on O'ahu (Wagner, Herbst, and Yee, this volume). Except for coastal wetlands, no vegetation zone is fully protected in more than 2 locations on any

Table 2. **Vegetation zones* included in Hawaiian protected natural areas, by island or island group.**

Island or Group	Vegetation Zone 4	A	B	C	D1	D2	D3	E1	E2	E3	5	6	7	8
Ni`ihau	--	--	--	--								--	--	--
Kaua`i	0/1	0/2	0/2	0/3	--	0/3	0/1				0/1	--	2/3	0/2
O`ahu	0/1	--	--	0/2	--	0/1	0/1				0/1	--	1/5	--
Moloka`i	--	--	1/0	1/0	--	1/0	1/0				1/0	1/0	1/0	1/0
Lana`i	--	--	--	--	--	--	--					--	--	--
Kaho`olawe	--	--	--	--								--		
Maui	2/0	--	--	1/0	1/0	2/0	2/0	2/0	2/0	2/0	1/0	2/1	2/1	1/0
Hawai`i	1/0	1/0	1/2	1/2	0/2	1/5	1/2	2/4	2/3	1/2	--	1/1	1/1	1/0
Offshore Islets	35/0													
Lee Hawaiian Islands	7/0	--	1/0											
Total	45/2	1/2	3/4	3/7	1/2	4/9	4/4	4/4	4/3	3/2	2/2	4/2	7/10	3/2

* See Appendix.

Legend:
-- none protected.
blank indicates habitat type does not occur on that island.
1/2 number of legally protected areas with active threat control program/number of areas with legal protection <u>or</u> active threat control.

island. All of Moloka'i's upland habitat protection is concentrated in a single protected area.

RARE SPECIES PROTECTION

Our protected natural areas should also include the fullest possible representation of the Hawaiian flora and fauna. There are difficulties in making accurate assessments of the species coverage of our natural areas, again due in part to the lack of survey data from large State-owned lands. Most current field information on rare plant and invertebrate species is in the heads of field biologists. There is no single respository or standard format for these data; thus, they are not available for protection planning. Nevertheless, examples from the major groups of organisms give a fair indication of our progress in Hawaiian species protection.

Of the 820 Hawaiian taxa included in *Federal Register* 45(242) (U.S. Fish and Wildlife Service 1980), approximately 125 or 15% are believed to occur within actively managed, legally protected natural areas. This does not include those plant species protected in arboreta. The Nature Conservancy's Heritage Program has recently compiled all available population data on 75 of O'ahu's rarest native plants. Of these, none have populations within a fully protected natural area.

Current protected natural areas include significant habitat for 10 of the 19 endangered or threatened Hawaiian forest birds. This legally and biologically protected habitat is probably adequate for long-term survival of only 3 rare bird taxa (Hawaiian goose; palila, *Loxioides bailleui*; and crested honeycreeper, *Palmeria dolei*) (Scott et al., in press). A significant portion of the essential habitat for endangered passerine birds on the island of Hawai'i is included within legally protected natural areas. However, only about 8% of this habitat is included in an active threat control program.

Hawaiian waterbirds and seabirds have received more protection than any other endangered group in their very limited remaining habitat. However, pressures on this remnant habitat are exceptionally great, and the manpower and funds available for threat control on many sanctuaries are very limited.

It is especially difficult to assess how much of our invertebrate fauna is included in protected areas, or to assess priorities for protection of particular taxa or habitat locations. Of 19 species in the endemic and endangered land snail genus *Achatinella*, none is protected in an area with an active control program for introduced predators, ungulates, or exotic plants. The only direct threat control program for Hawaiian land snails is at The Nature Conservancy's Kamakou Preserve on Moloka'i. This may be the only direct protection work under way for any terrestrial invertebrate in Hawai'i, and even this program must be described as "bare bones." Generally, invertebrates, more than other groups, must be indirectly protected by protecting their habitat.

Our native freshwater fauna owes any protection it currently enjoys primarily to the ruggedness or remoteness of remaining habitat. In the entire State, only one stream is legally protected and managed for the perpetuation of native species.

WHERE DO WE GO FROM HERE?

If it's an ark we're building as a legacy for the future, clearly we have a few missing passengers, and the boat is too small. The task before us now is to make the most of what we've already invested in natural areas protection, and of the limited resources available for the protection of additional areas. Here are a few suggestions.

1. We need to establish an ongoing data base to further determine which species and ecosystems are most in need of protection and where they can best be protected. This should be an objective source of standardized information accessible to all land use planners. At this point, we only have such data for Hawaiian birds. An essential part of this data base will be a definitive classification of Hawaiian ecosystems. Several agencies and organizations currently involved in collecting rare species data have met in order to coordinate their efforts into a product useful to all interested parties. This group includes the U.S. Fish and Wildlife Service, Bishop Museum Department of Botany, the State Division of Forestry and Wildlife, and The Nature Conservancy of Hawai'i. Once we have such a data base, we will be able to rewrite this paper and accurately represent just what and how much has been protected.

2. We need to support management (threat control) efforts for those priority ecosystems and species already included in legally protected natural areas. The commitment must be for long-term efforts. Specifically, we should:

(a) Plan and implement long-range threat control programs for all State NAR's. Priority natural areas presently in the conservation district but outside the NAR's should receive focused threat control through inclusion in the NAR system or through inclusion in a State Wildlife Sanctuary.

(b) Open selected NAR's and "Protected" Conservation Subzone lands to public hunters under liberal hunting seasons and bag limits as part of an ongoing program of ungulate reduction.

(c) Promote community volunteerism for active management of native elements in accessible areas such as State and county parks and some wildlife sanctuaries.

3. We need to provide perpetual legal protection for several areas well protected due to their natural isolation and ruggedness, before new disturbances greatly increase costs of long-term management. Examples are the Oloku'i Plateau on Moloka'i, Lihau Peak on West Maui, and several offshore islets. These are natural preserves requiring very little active management other than monitoring for alien species invasion. They also host some of our most intact native systems.

4. Clearly, additional areas need to be protected. In designing these, we need to include a commitment to perpetual management. This can be very costly, especially for an economy already stretched paper-thin over its present conservation programs.

5. To expect people to dedicate the resources necessary to fulfill this conservation commitment, we must improve the credibility of native species conservation. We must emphasize the importance of natural diversity to watershed quality, genetic resources, aesthetics, and local culture. And we must be prepared for the idea that we can't try to save every piece of land with Hawaiian species on it if we are to succeed in protecting the best remaining areas.

If a thousand years from today there are large areas of native landscape in Hawai'i, it will be because the people cared enough to save them, cared enough to keep natural areas protected even in the face of other potential uses for these lands. The long-term success that we all hope for depends on the people's appreciation of the land. The best prospect for making that future happen is to show today's people the value of our natural heritage and to show them how to care for it.

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APPENDIX

Overview of Ecological Zonation Scheme for the High Hawaiian Islands

Zonal Ecosystems [controlled dominantly through macroclimate]

1. Xerotropical (leeward lowland to submontane)

   A. Savannah and dry grassland [Prosopis savannah and Heteropogon-Rhynchelytrum grassland]

   B. Dryland sclerophyll forest (or scrub) [Metrosideros-Diospyros open forests; replacement vegetation: Leucaena scrub and forest]

   C. Mixed mesophytic forest (woodland or scrub). C1 low phase, C2 high phase. [Acacia koa open forests; replacement vegetation: Psidium guajava, Eugenia cumini forests or woodland]

2. Pluviotropical (windward lowland to upper montane)

   D1. Lowland rain forest [Metrosideros forests]

   D2. Montane rain forest [Metrosideros-Cibotium and dominantly Cibotium forests]

   D3. Upper montane rain or cloud forest [Cheirodendron or Acacia koa-Metrosideros mixed forests]

3. Cool tropical [upper montane to alpine; only on Maui and Hawai'i]

   E1. Mountain parkland and savannah [Acacia koa-Sophora chrysophylla tree communities, Deschampsia tussock grassland]

   E2. Subalpine forest and scrub [Sophora-Myoporum tree communities, Styphelia-Vaccinium-Dodonaea scrub communities]

   E3. Sparse alpine scrub [Styphelia, Vaccinium] and moss desert [Rhacomitrium lanuginosum var. pruinosum]

Azonal Ecosystems [controlled largely through edaphic factors]

4. Coastline
   . windward (beach, dune and rock substrates) [*Scaevola* scrub, *Pandanus* and *Hibiscus tiliaceus* forests]

   . leeward (beach, dune and rock substrates) [*Prosopis* scrub and woodland]

5. Bogs
   . low- and mid-elevation bogs

   . montane bogs [dwarf *Metrosideros*]

6. Geologically recent

   . vegetation on new volcanic materials [e.g. *Metrosideros*-*Sadleria*, *Gleichenia*, and *Lycopodium*]

   . lava tubes and other recent geological features

7. Aquatic

   . fresh water lakes

   . streams

   . coastal brackish and marine ponds

8. Cliffs

Note: Information synthesized by Gagne and Mueller-Dombois (n.d.) from earlier works. Letter symbols adapted to map in Ripperton and Hosaka (1942).

LITERATURE CITED

Gagne, W.C., and D. Mueller-Dombois. n.d. Synopsis of terrestrial vegetation types. B.P. Bishop Mus. and Univ. Hawaii Dep. Bot. Typescript.

Ripperton, J.C., and E.Y. Hosaka. 1942. Vegetation zones of Hawaii. Hawaii Agric. Exp. Stn. Bull. 89.

Scott, J.M., S. Mountainspring, F.L. Ramsey, and C.B. Kepler. In press. Forest bird communities of the Hawaiian Islands: their dynamics, ecology, and conservation. Stud. Avian Biol.

U.S. Fish and Wildlife Service. 1980. Endangered and threatened wildlife and plants; review of plant taxa for listing as endangered or threatened species. Fed. Register 45(242):82480- 82569.

Wagner, W.L., D. Herbst, and R.S.N. Yee. Status of the native flowering plants of the Hawaiian Islands. [This volume]

STATUS, RESEARCH, AND MANAGEMENT NEEDS OF THE NATIVE HAWAIIAN BIOTA: A SUMMARY

Stephen Mountainspring

The speakers in this session emphasized the uniqueness of Hawaiian plants, birds, and invertebrates. In each major group, over 95% of the resident native species are endemic to the archipelago. Native species have been heavily impacted by alien influences, first from the Polynesians beginning 1,500 years ago, then from the rest of the world following Cook's landing in 1778. Of the originally present birds, 70% are extinct; of the invertebrates, perhaps 50% are extinct; of the plants, 50% are candidates for the Federal endangered species register. Clearly, the native Hawaiian biota is highly susceptible to alien perturbations. It is most appropriate that impacts, research needs, and management strategies for the alien biota receive emphasis.

Several common themes run through the papers covering native biota. These points articulate the strategies needed to accomplish conservation objectives for different groups of organisms and are as follows:

1. A need for biosystematic studies.
2. A need for conservation status assessment (distribution and abundance).
3. A need for ecological studies (natural history).
4. A need for management action.
5. A need for public education.

These 5 interlocking topics constitute the basis for ensuring the ultimate preservation of native Hawaiian ecosystems.

Biosystematic studies are listed first because a correct understanding of which species we're dealing with is the first essential step towards our goal. This step has been nearly completed for Hawaiian birds; here we have an excellent idea of what the existing species are. For plants we have a great deal of information, but in many genera the knowledge of species limits or subspecific variation needs further and finer resolution. Presumably the forthcoming _Manual of the Flowering Plants of Hawai'i_ will begin remedying that situation. For invertebrates, particularly insects, species are far less well known; indeed, a complete inventory of the Hawaiian invertebrates is still lacking, despite Zimmerman's efforts that began after World War II and still continue.

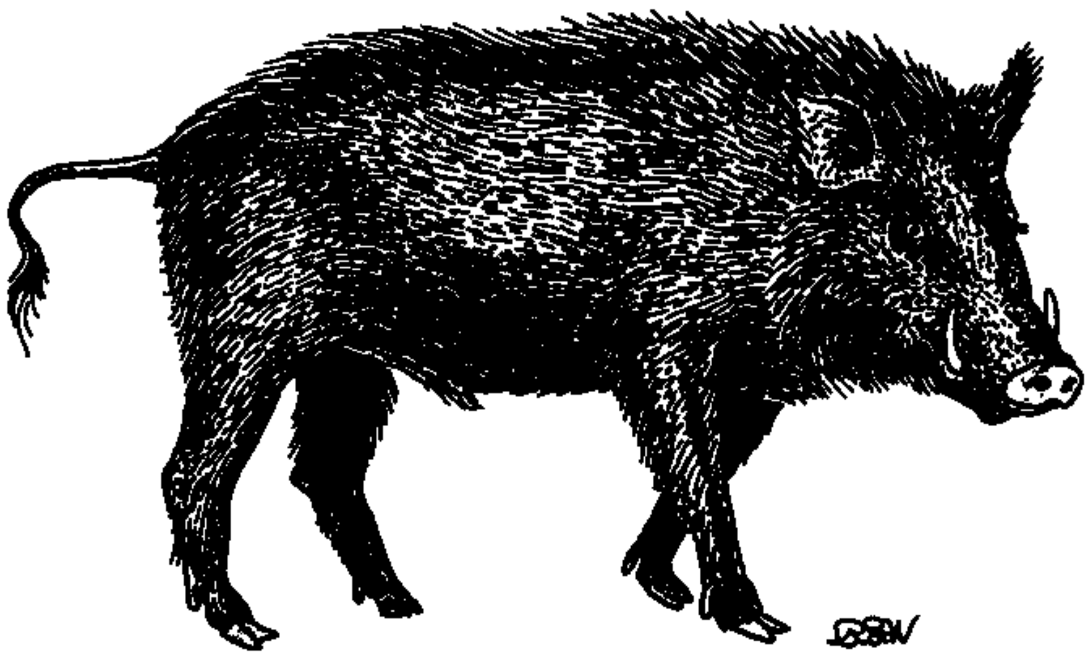
Once the taxa have been defined, the conservation status of each taxon can be determined. Before planning further research or management action, we need to know what species are rare, where their ranges lie, and in what habitats they occur. Through the efforts of the U.S. Fish and Wildlife Service, we have fairly good information about the distribution, abundance, and habitat response for forest birds on Hawai'i, Maui, Moloka'i, Lana'i, and Kaua'i, although even here the temporal component needs more sampling for seasonal and long-term trends. The Federal bird survey has also generated vegetation maps for the native montane forests of Hawai'i, Maui, Moloka'i, and Lana'i, but further mapping is needed on those islands for areas lying outside the distribution of native forest birds. Comprehensive mapping is needed for O'ahu and Kaua'i. Distribution data are available for most vascular plant taxa, and the Federal endangered candidate list offers at least a preliminary assessment of their conservation status. Good data on population structure, particularly regeneration, are still lacking for plants, and the recent discoveries of rare plant populations on East Maui and Kaua'i underscore the need for continuing systematic field surveys. When compared to that for birds and plants, our conservation knowledge of Hawaiian invertebrates is rather anecdotal and generalized. For certain well-studied groups there are good data, but most invertebrate species desperately require intensive and extensive study before we have a good understanding of their status.

Ecological studies are needed on all elements of the Hawaiian biota, including alien species, in order to understand and manage their impacts. Ecological studies are needed at 3 levels: the individual organism (autecology), the population (demecology), and the community (synecology). Individual natural history studies show us how the organism relates to its environment, and such studies are essential in identifying and quantifying the relative effects of different limiting factors. Studies of populations are important, first, in the conservation assessment of regeneration or reproduction, and second, in understanding the role of dominant or potentially disruptive species. For example, the concept of cohort senescence developed by Mueller-Dombois and his students, has forced us to re-evaluate the role of the 'ohi'a tree (_Metrosideros_ polymorpha) in montane forest ecosystems, and the studies of banana poka (Passiflora mollissima) and other alien plant species by Smith and his co-workers have proven essential in developing ecosystem management strategies. Population studies tend to grade into community studies when dealing with key species. The analyses by Jacobi and Scott (this volume) and Wagner, Herbst, and Yee (this volume) show that certain communities are especially rich repositories of native Hawaiian species, and some of these communities have been identified as highly threatened by disturbance. In communities such as the mature dry and mesic forests, some community types exist as single examples less than 25 hectares in extent, and effective conservation depends on understanding the relative role of the different disruptive influences on community stability and reproduction of the component species.

Management actions may be differentiated into 4 basic approaches: legal protection, management of alien (and occasionally indigenous) disruption, restoration of native ecosystems, and intensive management of individual organisms. As Holt and Fox reported in this session, 23% of the land in the Hawaiian Islands is legally dedicated to the conservation of native ecosystems, and 10% is subject to some sort of management program. Nonetheless, important parcels are missing from the dedicated lands, notably mesic montane koa (Acacia koa)-'ohi'a forests and mature low elevation dry woodlands. Moreover, the actual amount of land that is effectively managed to ensure continued reproduction of all key component species is very small--under 1%. Disruption of native ecosystems by alien elements such as feral ungulates, aggressive plants, rodents, invertebrates, and pathogens is nearly pervasive and demands such intense, focused attention to individual problems that generic solutions are still elusive. Protection and restoration are especially important in those communities retaining a high proportion of native components and natural processes. Although perhaps the most costly remedy, intensive management may be the only solution in some instances, such as for the 'alala or Hawaiian crow (Corvus hawaiiensis). Intensive management may be most feasible for certain rare plants, and some degree of success has been achieved by the National Park Service at Kipuka Puaulu in preserving Hibiscadelphus giffardianus and Zanthoxylum dipetalum as native components of the community.

As managers and researchers, we sometimes lack full appreciation for the importance of public education in furthering our conservation objectives. The general public and special interest groups are the ultimate sources of support for large-scale activities in conservation. Professional biologists need to repackage their formal findings into formats that lay audiences can readily assimilate. School and civic presentations are an essential component in getting the conservation message across and in elevating the general level of awareness of native ecosystems. Cultivating relationships with media reporters will also help the overall conservation mission, as will open dialogue between conservation agencies and other administrative and legislative bodies. We will be more effective at preserving native Hawaiian ecosystems as more people become interested in and aware of the value of their natural heritage.

II. STATUS, RESEARCH, AND MANAGEMENT NEEDS FOR ALIEN BIOTA



7.

IMPACTS OF ALIEN LAND ARTHROPODS AND MOLLUSKS ON NATIVE PLANTS AND ANIMALS IN HAWAI'I

Francis G. Howarth

ABSTRACT

Over 2,000 alien arthropod species and about 30 alien non-marine mollusks are established in the wild in Hawai'i. While the data are too meager to assess fully the impacts of any of these organisms on the native biota, the documentation suggests several areas of critical concern. Alien species feed directly on native plants or their products, thus competing with native herbivores and affecting host plants. Alien predators and parasites critically reduce the populations of many native species and seriously deplete the food resources of native predators. Some immigrant species spread diseases that infect elements of the native biota. Others are toxic to native predators. There is also competition for other resources, such as nesting and resting sites. Even apparently innocuous introduced species may provide food for alien predators, thus keeping predator populations high with an attendant greater impact on native prey. Control measures targeted at alien pests may be hazardous to natives. Mitigative measures must be based on sound research and firmer understanding of the complex interactions and dynamics of functioning ecosystems. Strict quarantine procedures are cost effective in preventing or delaying the establishment of potential pests. Strict control or fumigation is needed for nonessential importations (such as cow chips, Christmas trees, and flowers in bulk). Improved review of introductions for biological control is required in order to prevent repeating past mistakes. Biocontrol introductions must be used only for bona fide pests and used in native ecosystems only in special circumstances. Sufficient funds must be committed at the time of any intentional introduction for long-term monitoring of its efficacy and environmental impacts. Mitigation of other novel perturbations (e.g. land clearing, grazing, rooting by feral pigs (*Sus scrofa*), and invading weeds) that favor alien invertebrates will also lessen their impacts.

INTRODUCTION

It is quite appropriate to discuss the impacts of alien organisms at a conference on the natural history of Hawai'i, since Hawai'i ranks as one of the prime areas of the world in numbers of established alien species. This is true for both plants and animals (both vertebrate and invertebrate groups) as well as for intentional and inadvertent man-aided introductions (Lewin and Holmes 1971). The reasons for this distinction are diverse, and much speculation has been offered in explanation. Since the ecological reasons for the invasion of Hawai'i provide background that helps one to understand the impact of introduced species, I will briefly review the phenomena of colonization and establishment of aliens.

This paper focuses on the impacts of alien invertebrates. Alien plants, vertebrates, and avian diseases are discussed elsewhere in this volume. However, it must be stressed that the impacts and ecological problems are interrelated. That is, it is often the mix of alien species acting in consort or sometimes competitively that disrupts native ecological processes. This relationship should become more clear from the examples.

This paper is further limited to the insects and certain other arthropods and to terrestrial mollusks, because there is at least some published information available. Not treated are several phyla of worms and other lower invertebrates and many smaller groups of arthropods. This is unfortunate, as earthworms, for example, play a major role in soil formation; yet we know very little of the earthworm fauna and its role, if any, in prehuman Hawai'i.

Even among the insects the task at hand seems overwhelming. To date over 2,000 species have become established in the wild in Hawai'i and perhaps 20-30 new arrivals establish each year (Davis and Chong 1968; Beardsley 1979). In contrast, approximately 30 species of non-marine mollusks have been established in Hawai'i. However, in some cases their impacts on the native species are better documented than for other invertebrate groups. There have been few studies of the impacts of alien invertebrates on the native biota. Most of the published accounts are anecdotal or relate to single observations. Still, patterns emerge from these examples, and inferences can be made.

The biota of the Hawaiian Islands evolved in splendid isolation. Only those few unusually vagile or lucky groups that were able to cross thousands of kilometers of ocean colonized the Islands. Many arthropods, and especially the insects, are experts at long-distance dispersal. Thus, it should not be surprising that insects and their relatives are the dominant consumers on oceanic islands, particularly Hawai'i.

CHARACTERISTICS OF COLONIZING SPECIES

In order to establish a successful breeding population, a colonizing species must be pre-adapted genetically to exploit the resources in the new land. Potential hosts must be present in enough numbers and in the right developmental stage; nesting and roosting sites, reproductive cues, and other ecological requirements of the species must also be present; and climate, including properly cued seasonal changes, must fit the development of the colonizing species. Since the chances of both sexes being introduced simultaneously are low and the vagaries of finding a mate in the new land are high, hermaphroditic and parthenogenetic species have a much better chance of becoming established than do dioecious species (Howarth and Moore 1983). Indeed, a high proportion of alien invertebrates in Hawai'i can use one of the former types of reproductive strategies. It also follows that generalist species establish more easily than specialists, since the former, with their wider host or prey ranges, are more likely to find suitable food. The genetics related to colonizing ability and host specificity are becoming better understood, and this understanding leads to management and control recommendations (Carson and Ohta 1981; Templeton 1979; Schonewald-Cox, this volume).

Competition with already established species is important but not primary in determining whether a particular species establishes or not. That is, species packing (the number of species that can share or exploit a given resource) is a separate phenomenon from the establishment of a colonizing species. One of the outcomes of the Hawai'i International Biological Program (IBP) studies was the realization that, as more species become established in a habitat, it becomes more probable that additional species will find a suitable niche; thus, the chance of an alien species being able to establish is directly proportional to the number of species already present rather than inversely proportional, as is usually assumed (Mueller-Dombois and Howarth 1981).

A newly establishing species, however, often creates vacant niches within an ecosystem in that it or its products may not be initially exploited by the resident species. In time, either some resident species will adapt to exploit the alien, or other aliens will arrive to exploit it (Southwood 1960; Strong 1979;

Conner et al. 1980). This process is occurring in many lowland, man-disturbed habitats in Hawai'i, wherein the establishment of alien species is enhanced by the disturbance caused by humans or by introduced organisms. Each new alien further improves the chances of colonization by yet additional species.

Over one-third of the alien invertebrates in Hawai'i were intentionally introduced, mostly for potential control of pest species, but also for pollination, food, and other natural products. The rest were inadvertent introductions. These are the hitchhikers taking advantage of the improving human transportation facilities.

IMPACTS OF ALIEN INVERTEBRATES

Given the major role of invertebrates, especially insects, in nutrient cycling in natural ecosystems, especially those of oceanic islands, it seems axiomatic that alien invertebrates have the potential to cause serious disruptions. Our knowledge of island ecology is still insufficient to fully assess the effects of any alien species on the native biota. However, the meager data do indicate the magnitude of the problem. Alien invertebrates have invaded nearly every habitat so far studied in Hawai'i from the seacoast to the tops of the tallest mountains, and they affect every trophic level. Partial analyses of the invasion and role of alien species in 2 native Hawaiian ecosystems, the montane rain forest and caves, were presented in the IBP studies by Mueller-Dombois, Bridges, and Carson (1981). In this paper, the potential negative impacts of alien species will be described and illustrated with a few examples. Many of the examples must come from outside Hawai'i, since more research data are available there.

It may be too late to distinguish specific effects of aliens in many of the man-disturbed ecosystems in Hawai'i. Man is best adapted to the drier lowland coastal zone, and most of the plants and animals purposely brought in for food or other applications are, as would be expected, also adapted to this zone. These are the habitats most disturbed by man and his introductions; thus, as explained above, still further colonization of these areas is enhanced. This is also the zone in which new arrivals first find themselves on disembarking from planes or ships. Therefore, only species able to cope with climate and disturbance in port environs are likely to establish.

Direct Consumption of Native Plants

A large number of alien insects will feed on endemic plant species, sometimes doing extensive damage or causing severe defoliation. In most cases the plants recover, and the longer term effects remain unstudied or poorly known. Certainly, however, widespread defoliation or decrease in productivity of structurally dominant forest tree species, such as defoliation of mamane (Sophora chrysophylla) by the moth Uresiphita polygonalis (Conant 1975), and the effect on koa (Acacia koa) of the plant louse Psylla uncatoides (Leeper and Beardsley 1973), represent serious perturbations not only to the trees and their associated fauna and flora but also in hydrology, agronomy, nutrient cycling, etc.

Adults of the Chinese rose beetle (Adoretus sinicus) often congregate on favored hosts and characteristically create large rectangular holes in the leaves. Certain native plants are especially attractive and are jeopardized by depredations of this beetle, e.g. the proposed endangered Hibiscadelphus distans and Abutilon menziesii (Wagner, Herbst, and Yee, this volume).

Some generalist feeders, especially colonial or social species such as aphids, whiteflies, scale insects, and termites, may be reducing the ranges of certain native plants, but hard data are lacking in most cases. These abundant species contribute to the demise of the native lowland flora; the survivors from the human disturbance of fires, grazing, urbanization, agriculture, and competition from alien flora must also withstand an onslaught of alien phytophagous invertebrates building up populations on alien hosts.

Alien insect species are implicated as important factors in the decline and endangerment of a few plants. The black twig borer, Xylosandrus compactus, a tiny black ambrosia beetle (family Scolytidae) with an extremely wide host range, burrows into the growing tips and twigs of the host and introduces the pathogenic ambrosia fungus Fusarium solani, thereby severely pruning the host tree and often killing major branches or the whole tree (Hara and Beardsley 1979). Among its hosts in Hawai'i, of which 108 species in 44 families are known (Hara and Beardsley 1979), are several rare native species including Charpentiera sp., Claoxylon sandwicense, Drypetes phyllanthoides, Cryptocarya oahuensis, Alectryon sp., and Santalum freycinetianum. Gagne (1971) considered the borer to be the most important threat to the monarch of Hawaiian forests, Drypetes phyllanthoides; and Wagner, Herbst, and Yee (this volume) listed it among major factors in the endangerment of Gardenia brighamii and Mezoneuron kavaiense.

The black stink bug, Comptosoma xanthogramma (White), was first recorded in Hawai'i in 1966 and quickly threatened to become a serious pest of legumes, especially in the lowlands (Beardsley and Fluker 1967). During its initial J-shaped population curve in the decade following its arrival, it decimated the rare 'ohai, *Sesbanea tomentosa*.

Another example is the solanaceous treehopper *Antianthe expansa*, which was discovered on O'ahu in mid 1971. Its populations exploded on various cultivated and wild solanaceous hosts. By 1975 it was known from all the main Hawaiian Islands. High populations often killed susceptible hosts. Feeding records on native Solanaceae are lacking; however, alien species that have such wide host ranges within a plant family and that are able to build up large populations on alien weeds, are potentially serious threats to related native plants.

Among the alien mollusks, the slug *Milax gagates* is widespread and abundant in montane habitats. Gagne (1983) reported it feeding on greenswords (*Argyroxiphium* spp.) at 1,860 m in Haleakala National Park and felt that it was an important attractant, inducing rooting by feral pigs (*Sus scrofa*) in the fragile montane bogs. F.R. Warshauer (pers. comm.) considered slugs a serious threat to native ground orchids.

The attrition of the lowland populations of *Acacia koa* is augmented by the Formosan subterranean termite *Coptotermes formosanus*, which severely weakens older trees and shrubs. Since seed production in koa is being limited by predation by alien invertebrates and its seedlings are being defoliated by alien Lepidoptera and other herbivores, most of these fallen trees are not being replaced in the lowlands.

Significant direct interspecific competition for host plants should be most severe when food resources are limited. Many native insects are highly host specific and also may have quite restricted ranges. As their hosts decline due to a variety of environmental impacts, not the least of which are depredations of alien invertebrates, the native herbivores also decline. The currently listed endangered plants probably have already lost much of their associated arthropod fauna.

For example, in a status report on native moths, Gagne and Howarth (in press) regarded loss of host plant a major factor in the extinction of 5 species of Macrolepidoptera including *Hedylepta asaphombra* on *Joinvillea ascendens*, *Genophantis leahi* on *Euphorbia*, and the large hawkmoth *Manduca blackburni* on Solanaceae. The larvae (where known) of the curious endemic scythridid genus *Mapsidius* are restricted to the declining and localized populations of _Charpentiera_ spp. (Gagne and Howarth, in press).

Interference with Native Plant Reproduction

Seed predation may limit reproductive success of plants and thereby limit their distribution. In addition to the many native arthropods that are highly successful seed predators on native plants, there are in Hawai'i numerous alien groups that also specialize in seed predation. Some of these may directly compete with native seed feeders on some hosts, but their primary threat is the prevention of, or severe reduction in, reproductive success of the host.

Acacia _koa_ in drier areas appears to be limited in this way and may die out in such habitats. Predators may destroy over 85% of the seed production in koa, and in some (especially drier) habitats, koa reproduction is now almost never by seed (Stein 1983). Many ant species are also effective seed and seed sprout predators (Bond and Slingsby 1984).

Plants have evolved a variety of strategies to exploit local biotic or abiotic dispersal agents to move pollen from the anther to the stigma. The degree of outcrossing is important in maintaining variability and genetic fitness. The fact that a higher percentage of the Hawaiian flora has obligate outcrossing mechanisms compared with continental floras (Carlquist 1974) indicates a relatively greater reliance on indigenous pollinating mechanisms. Unfortunately, little work has been done on pollination biology among Hawaiian plants, although the role of birds has received some attention. Among the total native insect fauna there are perhaps a thousand species that habitually visit flowers and are potential pollinators. Many of these, including the yellow-faced bees, _Hylaeaus_ spp., and a great many moths, flies, beetles, and wasps, probably coevolved with elements of the flora to form mutualistic relationships.

Alien invertebrates have disrupted these pollination systems in several ways:

1. Changing the pattern of outcrossing among plant species, leading to a possible decrease in fitness or hybridization with relatives.
2. Theft of nectar from the plant, thus reducing the chance of pollination by legitimate visitors.
3. Reduction or extinction of coevolved pollinators leading to the decline of the plant cohort dependent on them.
4. Interspecific competition among pollinators for nectar resource, leading to the decline of the native species.

Foraging behavior among pollinators can be viewed as a dynamic strategy in which the caloric cost of foraging must be offset by the calories gained. Because pollination is important to agriculture, much research has been focused on modeling this energy equation. Different pollinator species may use widely different strategies to maximize their energy returns. Plants exploit these differences by adapting flower morphology and nectar production and composition in space and time to attract species that fit their own reproductive strategies. The parameters involved include foraging ranges, number of flowers visited per trip, floral constancy, genetic outcrossing, climatic limits, nectar composition, and competitive behavior.

The most important introduced invertebrate pollinator is, of course, the European honey bee, Apis mellifera. This species was purposely brought to Hawai'i about 1875 as a honey producer and pollinator. It quickly naturalized in native and alien habitats from the sea coast to near the tree line. Its large sophisticated colony confers on it a foraging strategy very different from that of any of the native pollinators; it seems likely that it has disrupted the natural reproductive patterns of many native plant species, but there are no data to support or refute this. Honey bee colonies are very efficient at exploiting high quality resources such as a tree with massive blooming. Scouts locate nectar sources and return to the hive to recruit foragers which concentrate on that source until it is exhausted. Thus, for some massively blooming trees, outcrossings may be reduced. On the other hand, the large colony, exchange of pollen among workers, the wide ranging foraging, and the catholic (generalist) tastes of the bees mean that pollen from quite varied genetic sources may be carried by Apis workers (Roubik and Buchman 1984). Perhaps some of the hybrid swarms now seen among native floral groups are the result of indiscriminate outcrossing pollination.

In Central America, low colony densities of the alien Apis mellifera did not appear to adversely reduce the colony vigor of several sympatric native social bees, even though there was considerable overlap in plant species visited. Many of the foraging strategies employed by both the native bees and the honey bee probably developed through intercolony competition (Roubik 1983). Curiously, in Central America the honey bee is able to exploit many native plants (Roubik 1983), whereas in New Zealand this species forages predominantly on introduced plants (Donovan 1980). In Central America there are many native social bee species, and many of the floral taxa have coevolved to exploit the foraging behavior of colonial species. In contrast, New Zealand has a diverse assemblage of primitive solitary bees only, and the native flora evolved without the influence of colonial pollinators. Hawai'i is similar to New Zealand in that there is only one native group of solitary bees, albeit a speciose one with more than 60 known species.

One big competitive advantage of social species like the honey bee over most other pollinators, including birds and other bee species, is that large honey stores permit them to wait out bad times and rapidly recruit foragers to exploit newly developing resources (Roubik and Buchman 1984).

Little is known of the potential impacts of other alien pollinators. The 4-5 alien bee species besides the honey bee are generally lowland, open-habitat species and probably mostly associate with alien plant species. The large carpenter bee Xylocopa sonorina aggressively robs nectar from many sympetalate flowers (Gerling 1983). Mostly introduced ornamentals are affected, but some lowland native populations of Hibiscus, Ipomea, and others may also be attacked. Not only are robbed flowers less likely to be pollinated, but such flowers and the plant are less likely to be visited by legitimate pollinators.

Ants, particularly Pheidole megacephala, are also notorious nectar robbers. Their aggressive defense of food sources acts to deter other species from using the flower. Many plants have evolved a variety of defenses, such as hirsute stems, in order to reduce loss from ants and other robbers. Ants were not part of the native fauna, and some native plants may be quite vulnerable to their impact.

Although direct competition among alien and native pollinators may reduce populations of some natives, the indirect results of habitat loss (particularly nesting sites) and predation on native pollinators by alien invertebrates have reduced their numbers even further. At the same time, with the loss of such a large percentage of the native plant cover from lowland habitats (Wagner, Herbst, and Yee, this volume), many coevolved systems have been interrupted, i.e. either the plant or the pollinator species populations became too low to maintain the other, and one or both became extinct. The endemic yellow-faced bees appear to be greatly reduced in both species and numbers of individuals from Perkins' day (Perkins 1913).

Predation and Parasitism of Native Animals

A large proportion of alien invertebrates is predaceous or parasitic. Two principal factors are responsible. First, generalist species in the higher trophic levels often become established more easily than other guilds (Mueller-Dombois and Howarth 1981), and therefore a relatively high number of predators and parasites are characteristic of island faunas (Janzen 1973). Secondly, the popularity of purposeful introductions for biological control resulted in a large number of entomophagous species being imported and released.

Alien predators and parasites have had disastrous impacts on native organisms (Zimmerman 1948, 1958; Solem 1976; Wells, Pyle, and Collins 1983; Howarth 1983; Gagne and Howarth in press), but space allows only a few better documented examples to be given here. The environmental risks present in biocontrol introductions were reviewed by Howarth (1983), Pimentel et al. (in press), and Gagne and Howarth (in press). These will be discussed below. More species extinctions can be attributed to the impact of species imported for biocontrol than can be attributed to the much more maligned chemical control (see also Honneger 1981; Pyle, Bentzien, and Opler 1981; Clarke, Murray, and Johnson 1984).

Of the alien invertebrate predators, ants, particularly the big-headed ant, are the most notorious and have been most implicated in the extinction of native species in Hawai'i (Zimmerman 1948; Solem 1976; Gagne 1979; Hardy 1981). Even though there have been few controlled studies on their impacts on native ecosystems, the circumstantial evidence is clearly incriminating. All of the 35-40 species of ants currently established in Hawai'i are alien, and most of them are distributed mainly in lowland tropical or disturbed open habitats (Huddleston and Fluker 1968). Most are also cryptic, nocturnal, and nest in soil or wood cavities; therefore, their biologies and impacts remain poorly known. Several species are common and widespread and may become locally dominant (Huddleston and Fluker 1968). However, it is the aggressive species with larger colonies that have the most potential for harm. In Hawai'i these include the big-headed ant, Argentine ant (<u>Iridomyrmex humilis</u>), long-legged ant (<u>Anoplolepis longipes</u>), and the fire ants (<u>Solenopsis geminata</u> and <u>S.</u> sp. "A") (Huddleston and Fluker 1968). <u>I. humilis</u> and <u>A. longipes</u> have not yet reached their full potential range in Hawai'i and pose grave threats to the native fauna (Hardy 1981; Fellers and Fellers 1983).

Social predators are not present in the native fauna, and wherever these aggressive ants are common, nearly all of the exposed, naive native arthropods are threatened, as the native fauna evolved in the absence of such a foraging style and is now vulnerable. Gagne (1979), in his study of arthropods associated with 'ohi'a (Metrosideros polymorpha), found only species resistant to ant predation in areas where ants were common. Among native species were gall makers, borers, vagile species able to escape, and those with repugnatorial scent glands. Flightless native species, particularly predators, are believed to be most vulnerable (Zimmerman 1948; Fellers and Fellers 1983; Hardy and Delfinado 1974). Ants can competitively exclude some predators by efficiently consuming most of their prey (Risch and Carrol 1982; Lubin 1984). Perkins (1913) noted the near absence of native arthropods, especially beetles, where ants were numerous. Solem (1976) felt that ant predation was a major factor in the extinction of Hawai'i's endemic endodontid land snails.

Ants feed primarily on food rich in energy or proteins, such as honeydew, nectar, seeds, live prey, and carrion. Their colonial lifestyle with chemical communication allows rapid recruitment at and exploitation of high density food resources. Workers continue to gather food even though physiologically satiated (Risch and Carrol 1982), and excess food is stored in the colony (usually as increased brood). If food supply wanes, the brood is cannibalized. In this way the colony can withstand tremendous fluctuations in food supply.

The impacts of ants on animal populations are far greater than would be predicted from the number of prey consumed, since worker numbers and pugnacious behavior discourage other organisms from foraging, feeding, or roosting in ant-infested areas. Disruption of pollination has already been mentioned. Other examples are prevention of parasitism and predation of honeydew-producing homopterans, discouragement of feeding of herbivores, and disturbance of small animals from their hiding places. In the Galapagos, Lubin (1984) found that the alien little fire ant, Wasmania auropunctata, was able to displace and extirpate not only several other ant species, including the endemics, but also several spiders and a scorpion.

Recently 2 species of vespid wasps, the yellowjackets, also social predators with large colonies, entered Hawai'i. Both are temperate zone forest species that have extremely catholic tastes. Unfortunately, they pose a grave threat for many native species living in upland forests. Underscoring the importance of genetic makeup to the success of colonizing species, one of these wasps, Vespula vulgaris, is a boreal species and generally prefers coniferous forests. It also appears to have a strong seasonally controlled diapause and is only weakly established in Hawai'i. The other species, V. pensylvanica, is much more plastic and has been able to invade upland mesic forests and alpine scrub. The problem race of V. pensylvanica was first reported in 1977 and subsequently rapidly spread throughout the islands (Nakahara 1980). Its J-shaped population curve corresponded to an alarming decline in several native groups, notably Drosophila (Wells, Pyle and Collins 1983; H.L. Carson, pers. comm.), and Lepidoptera (S.M. Gon, III and W.P. Mull, pers. comm.). The huge colonies, sometimes a meter or more in diameter, represent significant numbers of consumed prey.

V. pensylvanica is currently in decline or stable in most areas, suggesting that food may have become limiting (i.e., the more naive prey are now so low in numbers as not to support as large a population of wasps) or that other intrinsic or extrinsic factors are limiting their populations. The indirect impacts on other predators, notably the native forest birds, were apparently not studied during the wasp's high population phase. Breeding success in passerines is generally related to availability of suitable prey items, which for the native species include caterpillars and other arthropods known to be prey of Vespula. The aggressive stinging behavior of the wasp may also have affected naive native animals. The native solitary diurnal predatory wasps, e.g. Odynerus spp. and Ectemnius spp., which share many prey species with Vespula, also would be expected to be severely affected.

Zimmerman (1958) lamented the loss of Hawai'i's moth fauna thusly: "The importation of parasites to control various moths of economic importance, together with the accidental importation of other parasites has resulted in wholesale slaughter and near or complete extermination of countless species. It is now impossible to see the Hawaiian Lepidoptera in the natural proliferation of species and individuals of Perkins' day. Many are forever lost." Zimmerman (1948) also believed that the reduction of native caterpillars led to the rarity and perhaps extinction of native predators, especially Odynerus wasps.

Since the mid 1950's 3 predatory snails (Gonaxis kibweziensis, G. quadrilateralis, and Euglandina rosea) have been introduced into Hawai'i in hopes of reducing populations of the pestiferous giant African snail (Achatina fulica). Of these, E. rosea has been most seriously implicated in the extinction of many native tree snails including the endangered genus Achatinella. Hadfield and Mountain (1981) presented good evidence demonstrating that the demise and complete extirpation of a well-studied population of Achatinella mustelina coincided with the arrival and multiplication of E. rosea in their study site. Their study confirms the circumstantial evidence and dire predictions made by van der Schalie (1969) and others.

Unfortunately, the same scenario is being replayed on other Pacific Islands as these predatory snails are still being spread purposefully by well-intentioned but misinformed individuals who hope to control the giant African snail (Wells, Pyle, and Collins 1983; Tillier and Clarke 1983; Clarke, Murray, and Johnson 1984). These introductions continue even though the efficacy of E. rosea for the control of populations of A. fulica has not been rigorously demonstrated. For example, populations of A. fulica often decline in the absence of E. rosea (Mead 1961, 1979; Tillier and Clarke 1983; Christensen 1984; Clarke, Murray, and Johnson 1984).

Populations of native tree snails appear to be strongly negatively correlated with populations of the alien garlic snail, Oxychilus alliarius, in many habitats on Maui (Severns 1984). This species is apparently an omnivore and opportunistic predator, and sometimes reaches incredible populations in forest leaf litter.

Birds and their nests harbor a large and diverse assemblage of parasitic and nidicolous invertebrates. Several of the alien species in Hawai'i potentially are important blood sucking parasites on native birds, but studies are few. Goff (1980b) found the northern fowl mite, Ornithonyssus sylviarum, on the house finch (Carpodacus mexicanus) in Hawai'i Volcanoes National Park. Besides their potential for disease transmission among native forest birds, this and related species, especially the tropical fowl mite, O. bursa, and the chicken mite, Dermanyssus gallinae, are known to decrease vigor and disrupt fledging success in their hosts by exsanguination.

Transmission of Disease Organisms Among Native Biota

Alien invertebrates, especially mosquitoes, that transmit avian diseases among naive native birds are considered to be among the more serious threats to the survival of some species. This is one of the better documented impacts of alien invertebrates on native species (see van Riper and van Riper, this volume), but further studies are needed.

Alien invertebrates also vector plant diseases, and some of these pose serious threats to native flora. The black twig borer's role in transmitting a pathogenic fungus has already been described above. The demise of the American elm (Ulmus americana) as a result of the Dutch elm disease spread by related beetles in North America shows that this problem is not confined to islands. The alien koa psyllid Psylla uncatoides was incriminated by Leeper and Beardsley (1973) in the mechanical transmission of native koa rusts, Uromyces spp., on Acacia koa and the potentially endangered *A. koaia*. Here is an example of a native group of diseases that appears to have become more virulent on native hosts when a more efficient vector became established. However, much of the dieback of the host trees was attributed to the feeding injury of the psyllid rather than to the rusts (Leeper and Beardsley 1977).

Insects and plant-feeding mites are particularly well adapted to transmitting a great variety of plant diseases, and much work has been done on their role in agricultural systems. Very little has been done in natural systems in Hawai'i, but a relatively large number of alien arthropods, such as aphids, leaf-hoppers, true bugs, and mites, belong to groups known to be efficient vectors.

Alien invertebrates may harbor alien diseases and act as carriers or reservoir hosts, i.e. tiny "Typhoid Marys", facilitating the spread of these diseases among susceptible hosts. The problem is poorly researched in Hawai'i, but may account for the disappearance of certain native groups. Native crayfishes (Astacidae) in Europe are being extirpated and driven to the brink of extinction by the fungus disease caused by *Aphanomyces astaci*, and disseminated by the introduced North American crayfishes *Procambarus clarkii* and *Pacifastacus leniusulus*. Both native and alien crayfishes are susceptible, but a higher percentage of aliens survives. Some of the survivors become resistant and act as reservoirs or carriers for new epizootics. Given the high reproductive rate of the alien species and their higher survival rate from this alien disease, the alien species become more and more numerous at the expense of native species after each epizootic phase and each generation (Wells, Pyle, and Collins 1983).

A similar process may be occurring here in the leaf litter with the alien sandhopper *Talitroides topitotum* and the native talitrid sandhoppers. *T. topitotum* has nearly replaced native species in the leaf litter in most areas below 1,000 m in Hawai'i. In New Zealand where *T. topitotum* is still spreading, it is also replacing the native species, apparently in large part by the interaction of an alien milky disease and amphipod populations (K.W. Duncan, pers. comm.). A similar milky disease is present in *T. topitotum* in Hawai'i.

Mead (1961, 1979) postulated from field observations in Hawai'i that a bacterium, *Aeromonas* sp., was the main factor controlling populations of the giant African snail. The rat lungworm *Angiostrongylus cantonensis* also is known to infect a broad range of snails. These diseases could be a factor in the decline of native snails.

Synergistic Effects among Aliens

Often 2 or more harmful alien species may act in consort so that their joint impact is more severe than that of the several species acting separately. Even an otherwise innocuous or seemingly beneficial alien may, in fact, act in consort with other aliens with a consequent synergistic effect, causing great harm to the native biota.

Alien invertebrates may be food resources for alien predators, may pollinate alien plants, may disperse alien plant propagules, may tend and disperse alien herbivores, and may alter soil structure. All of these activities will tend to favor certain alien species at the expense of natives. In the more disturbed habitats where large numbers of aliens have become established, many if not most of the ecological processes within the community are now carried out by aliens. Without intensive artificial management, native species are at a great disadvantage in these areas.

Many pestiferous ant species tend alien honeydew-producing homopterans, such as aphids, mealy bugs, and treehoppers. Nearly 50 species of potentially pestiferous honeydew producers have become established. Many are host specific and mainly attack alien plants. Others are more catholic feeders and are important herbivores feeding on native species. Many of these alien honeydew producers require mutualistic ants for efficiently protecting them from predators and dispersing them from plant to plant. The ants gain from them an abundant food supply, and, in fact, some of the most pestiferous ant species would possibly not have become established had not suitable honeydew-producing species already been present. Furthermore, the ants in general might not have become such a problem to native species had they not been able to exploit these plant-sucking bugs. It may be that the ranges of some alien ant species are restricted at present because of the absence or rarity of suitable honeydew-producing species in certain areas.

Another case of synergism exists among scarab dung beetles, mongooses (Herpestes auropunctatus) and cattle. Several scarabs were intentionally introduced to remove cow dung from pastures, thereby allowing grasses to regenerate and reducing the larval food of the horn fly (Haematobia irritans), a pest of cattle. Not only do the beetles thus favor invasion of Hawaiian ecosystems by cattle, they also are an important food source for the mongoose, especially in upland pastures. In fact, the mongoose might not maintain high populations in pastures and neighboring areas without the dung beetles (Tomich 1969). Pimentel et al. (in press) thought that the mongoose actually favors the population of the roof rat (Rattus rattus) in Puerto Rico by reducing its ground-dwelling competitor, the Norway rat (R. norvegicus).

Alien invertebrates are important pollinators of alien plants, including weeds. The honey bee probably plays an important role in successful seed set for a great many alien species, including some weeds. Several species of the obligate, specific pollinators of fig trees, including potential weed species, were intentionally introduced. These never would have escaped from cultivation had their specific wasp pollinators not been introduced. One of the major reasons more of the thousands of alien species of orchids and other ornamental plants have not escaped cultivation is that their specific pollinators have not become established. If an effective pollinator is introduced, the pollinated plants might escape cultivation and become a problem in native ecosystems.

A few higher plants are dispersed by arthropods, and ants are the most important agents. The role of myrmecochory (seed dispersal by ants) in the distribution of weedy aliens deserves more study. Hawai'i has no native ants, and thus is not expected to have ant-dispersed plants among the native flora. In South Africa the alien Argentine ant (a species also alien in Hawai'i) is disrupting the seed dispersal of several native myrmecochorous plants and may eventually cause their extinction (Bond and Slingsby 1984).

Alteration in Soil Formation and Structure

Invertebrates, especially earthworms, play a major role in soil formation and structure. Unfortunately, I have not been able to review the impacts of alien earthworms, nor is there much information on the role of native soil organisms. Colonial soil insects, such as termites and ants, greatly alter the soil in the vicinity of their nests, and few plants (possibly all of them aliens) thrive in such areas.

Termites greatly increase the breakdown rate of woody material and thus may make some plant nutrients less available to native species. The role of dung beetles (and other alien dung feeders) in cleaning up cow feces has already been mentioned. Few native invertebrates can exploit the dung of alien vertebrates. The incredible populations achieved by some alien invertebrates in certain habitats, e.g. isopods, millipedes, the garlic snail, and some ants, represent significant changes in the nutrient cycling process even if their direct impacts are obscure.

Hybridization with Related Native Forms

If the alien has a close relative among the native fauna, hybridization is possible, with the possible swamping and eventual extinction of the island species (Wells, Pyle, and Collins 1983). Hardwick (1965) presented morphological evidence that the alien corn earworm *Helicoverpa zea* population on Laysan Island may have introgressed with an undescribed native species. He also believed that the apparent extinction of the related endemic species *H. confusa* from the main Hawaiian Islands may have been due to aggressive males of *H. zea* becoming locked *in copula* during attempts to mate with *H. confusa* females. Under this scenario an increasingly larger percentage of *H. confusa* females would have been removed from the population with each generation.

Effects of Alien Pest Control

Finally, alien invertebrates interfere with human endeavors in the Islands. This competition often leads to chemical and biological control procedures. Chemical applications also may kill native species and pollute the ground and water resources, impacting native species living there. Biocontrol introductions sometimes also attack native species. Perhaps the most notorious examples are the alien fruit flies. These pests have provoked proposals of massive eradication schemes, some of which have been attempted, including intensive aerial spraying of large parts of the island of Lana'i with broad-spectrum pesticides. In addition, over 2 dozen species of predators and parasites, some of which now attack native arthropods, have been introduced.

Control of alien pestiferous mosquitoes has included draining and chemically treating wetlands, with attendant environmental problems, as well as the introduction of mosquito fishes (*Gambusia* spp.) to numerous water bodies in the State. This spread of predatory fishes continues today even into remote areas, despite the fact that these generalist predators are known to severely disrupt native aquatic life (Haas and Pal 1984), including extirpating the rare damselfly *Megalagrion pacificum* from many areas (Moore and Gagne 1982).

SOLUTIONS

With so many alien species established in Hawai'i and their impacts so pervasive, the initial reaction is to throw up one's hands and say that we are too late to save much of Hawai'i's biota. However, native species display a resilience in the face of these new destructive forces, and many spectacular natives still survive, a fact that is stressed in other papers in this Symposium. Such recent biological discoveries in

Hawai'i as the cave and aeolian ecosystems, raptorial predatory caterpillars, hundreds of new species of arthropods, a new extant bird species, and new information on the evolutionary biology of Drosophila, should instill new conviction that Hawai'i's native biota deserves protection and management. Recent studies demonstrate that native ecosystems will benefit from protective management (Muller-Dombois, Bridges, and Carson 1981).

The Hawaiian biota coevolved with a diverse and rapidly evolving invertebrate fauna. Thus, numerous elements would be expected to be resistant to many of the threats posed by alien invertebrates. As an example, the resistance of Hawaiian cotton to bollworms (Helicoverpa spp.) is being incorporated into some commercial strains of cotton. However, it appears that certain forms of novel alien threats, i.e. those with which segments of the native biota have no previous contact or with which they were not preadapted to cope, may create irreversible changes.

It is clear from this review that social and colonial species of invertebrates--termites, ants, bees, wasps--are by far the most damaging to native species. Disease transmitters are also a serious concern. Generalist species within each trophic level are nearly always more damaging to native communities than are specialists. These attributes can provide a sound predictive basis for assessing potential impacts of new arrivals as well as for establishing guidelines in reviewing proposals for releases for biocontrol or other purposes.

Quarantines

Probably the most cost-effective measure to reduce the negative impacts of alien invertebrates in the Islands is to stiffen quarantine procedures in order to greatly lessen the chance that a harmful alien will be intentionally or inadvertently introduced. Quarantine cannot hope to be absolute in keeping everything out, but it is a method to buy time between crises and allow for the development of management strategies.

In order to be effective, quarantine regulations must be strictly enforced. Public education campaigns must stress the fact that quarantine protects everybody, i.e. the State's economy, the public's health, and the environment. Proper education can make enforcement palatable to travellers. It must, or we have lost. For the harmful aliens we have now are but minor previews of the impacts of a whole host of invertebrates waiting for a ride to our shores. For example, in terms of conspicuousness and extent of negative impacts, Hawai'i so far has fortunately escaped as damaging an alien invertebrate as the gypsy moth in North America (Marshall 1981).

The great isolation of Hawai'i will aid quarantine efforts, for transportation possibilities are limited to long-distance boats and aircraft. These, both military and civilian, must be closely inspected and also treated to prevent the escape of invertebrate stowaways. The immediate areas surrounding ports of entry, such as piers and airports, should be treated to minimize establishment and monitored for incipient infestations, the latter to be dealt with promptly. Shipments of economic commodities and personal goods should be inspected or fumigated as appropriate by qualified personnel.

Nonsensical importations, i.e. importations that have a high risk of harboring pest species and either are non-economical (recreational) or directly compete with a viable local industry, deserve special scrutiny. Some of these appear ludicrous. Dried cow dung, which harbors an unbelievable array of blood-sucking and other arthropod pests, has been imported for cow chip throwing contests. Polo ponies have been air freighted in luxury without quarantine directly between games all over the world (several recent coprophages almost surely arrived by this jet set polo route). Boatloads of untreated Christmas trees arrive every winter with an alarming array of hibernating or diapausing pests. Cut flowers for the lei and florist trade are air-freighted in bulk from other tropical areas, especially the Philippines. Zoo animals, recently especially reptiles, have arrived without quarantine, creating a number of incipient infestations of bloodsucking mites at the zoo and elsewhere in Honolulu (Goff 1980a). Plants and animals are being imported for the home aquarium and pet trade. And finally, plant propagules are shipped in for the botanic gardens and florists, often with their associated fauna still attached. All of these are classed as high risk in regard to the arrival of alien pests, and indeed several recent pests have arrived by each of these routes, including kissing bugs, chiggers, ticks, sepsid dung flies, spiraling whiteflies, plant bugs, and flower-feeding moths. The promoters of high risk importations must recognize that strict measures assuring the absence of alien stowaways must be applied or the activity must be curtailed.

Quarantining living plant importations makes good sense, since great numbers of plant-associated invertebrates have a cryptic stage, either inside or on their host plant. For example, insect eggs are often cryptically attached to the plant and many species actually insert their eggs into plant tissues. These are very difficult or nearly impossible to detect during inspections.

In addition, bulk shipments of certain fresh produce should be regulated to prevent harmful introductions. For example, shipments of watercress, particularly, often harbor an array of potentially detrimental species of snails and slugs (C.C. Christensen, pers. comm.). Since watercress is also produced locally, curtailing its importation would seem to benefit the local economy, as well as reduce the threat of importing pests.

Research Needs

Measures to lessen the impact of alien invertebrates must be based on sound research and firm understanding of ecosystem processes and functioning. Basic to understanding and subsequent management of Hawaiian ecosystems is the need for a more thorough biological survey. Most groups of native insects and other invertebrates are still poorly known taxonomically, even though these groups play a greater role in ecosystem function than they do in analogous continental ecosystems. Management procedures are impossible if the managers cannot recognize or distinguish native from alien species.

Long-term basic ecological studies are required because ecosystem models ideally must be able to distinguish temporary shifts in populations from the more serious irreversible changes in response to new perturbations. Ecosystems are dynamic mosaics of species interacting in complex food webs. Each species is continually adapting and evolving in response to ever-changing biotic and abiotic selective forces.

A number of ecological problems, which require research data before they can be solved, were identified in this review. Among the more critical is the need to monitor the spread and impacts of ants and other highly damaging aliens in Hawaiian ecosystems. More experimental long-term research is especially needed on the autecology of these aliens in order to find their weaknesses, develop environmentally sound but effective controls, and implement mitigative procedures. Studies are needed on the efficacy and environmental impacts of species imported and released for biological control.

Long-term autecological studies are also needed on the rarer or more interesting segments of the native biota, especially invertebrates. Much useful information can come from such studies. For example, Hadfield and Mountain (1981) found that the slow growth rate of the tree snail *Achatinella mustelina* and its low fecundity left it extremely vulnerable to predation pressures. The next step is to find mitigative measures to reduce predation by alien species.

Research data are also needed on the relationships among alien diseases, vectors, reservoirs, and the native biota. Studies on pollination and reproductive strategies of both native and alien flora might provide information leading to the development of management strategies for protecting native species. Additionally, the inclusion of invertebrate surveys and assessment in the environmental impact statement (EIS) process is strongly recommended.

<u>Management</u>

Management recommendations for mitigation of the impacts of alien invertebrates already established center mostly on reducing the novel perturbations that favor populations of the aliens. Our ecological experience is not yet sophisticated enough to propose specific, environmentally sound measures for most problems concerning alien invertebrates. The special constraints of biocontrol will be discussed separately.

A number of alien leaf litter and soil invertebrates are favored by the disturbance caused by feral vertebrates, especially rooting by feral pigs. The relationship among cattle, dung beetles, and mongooses was described above. Reduction of feral vertebrate perturbations will also reduce the impacts of these aliens. Invading alien plants provide food and avenues for the invasion of the forests by alien arthropods. This presents greater opportunities for interactions among these alien invertebrates and native species.

Certain ants and yellowjackets pose severe threats and require special controls in native habitats. In national and state parks, in natural area reserves, and in accessible areas such as along public trails, yellowjacket nests should be searched for and destroyed. Efficient methods of locating nests need to be developed, and their populations should be monitored and further control measures taken wherever their activity increases.

Several of the alien ants are best adapted to exploit disturbed ecosystems, especially continuously cropped agroecosystems (Risch and Carrol 1982; Lubin 1984). This may be related to availability of suitable nesting sites, incomplete ground cover, shorter stature of vegetation, or competition. Removal of disturbances such as grazing by feral ungulates, fire, and forest clearing may minimize or reduce the impacts of these alien predators and slow their spread into forest ecosystems.

The alpine scrub vegetation zone (E2 and E3 in Ripperton and Hosaka 1942), with its low stature plants and abundant rocky substrate, presents an ideal habitat for those ants that can withstand the harsh climate. The possibility that the Argentine ant will establish in Haleakala Crater and do irreparable damage is further enhanced by the presence of large colonies of aphids on alien weeds such as the oenothera aphid Aphis oestlundi on the evening primrose. Research on management of these weeds should begin now before a crisis occurs. In addition, these aphid colonies may provide a handy monitoring station for early detection of the establishment of any of the harmful honeydew-tending ants. The colonies of the Argentine ant near Park headquarters and at Kalahuku should be contained and eradicated if possible. Material, especially that stored on the ground in infested areas (e.g. fencing equipment), should be closely inspected before being carried into Haleakala Crater (Beardsley 1980). An assessment of the status of native invertebrates and plants within the outside areas occupied by the Argentine ant near Park headquarters would provide documentation of the urgency of the problem in this habitat (Beardsley 1980; Fellers and Fellers 1983).

Monitoring the activity of the long-legged ant in lower Kipahulu Valley and research on control is necessary to assure the survival of the native stream fauna there (Hardy 1981), which includes the last known population of the rare and endangered damselfly Megalagrion pacificum.

Biocontrol

The major aegis for purposeful introduction of invertebrates into Hawai'i has been classical biological control (the discovery, importation, and release of an alien species with the expectation that it will control a "pest" population). The method blossomed in Hawai'i in the late 19th and early 20th centuries, largely through the activities of one man, Albert Koebele. There have been some apparent spectacular successes in the control of both weed and animal pests. Records for species introduced are scanty, especially for the early years as Koebele and probably others only recorded those that they felt were successful (Swezey 1931). To date probably over 2,000 invertebrate species have been intentionally imported for biocontrol, but only a part, between 10 and 25%, actually have become established.

Now that the environmental risks of classical biocontrol are recognized, we need to reevalute the methodology and philosophy used by workers in this area (Howarth 1983; Klingman and Coulson 1983; Haas and Pal 1984; Pimentel et al., in press). It must be stressed here, however, that this in no way is meant as criticism of the activities of past or current workers in biocontrol. Biocontrol specialists acted with the best information and rationale available at the time and did what was thought to be in the best interests of human welfare and agricultural and economic development. As with any applied science, biocontrol must change to accommodate the new empirical and theoretical data in order to advance as a discipline. Historically, Hawai'i has been a world leader in developing empirical methodologies and in advancing the theory of biocontrol. It is heartening to note that Hawai'i's agriculturalists are modifying their standard operating procedures in order to address and minimize newly recognized risks.

In a comparison of environmental concerns among pest control procedures, I listed 6 limitations of classical biological control (Howarth 1983). These were that:

1. Classical biocontrol procedures are usually irreversible.
2. The imported organisms may expand their host range and attack non-target organisms.
3. The imported organisms may spread and invade other habitats.
4. The method has been plagued by poor research design on efficacy and environmental impact analyses.
5. Biocontrol needs a better review of cost-benefit analysis.
6. The method requires adequate sophisticated biosystematic and ecological data on both the target species and the control species.

The first priority in control should be understanding the ecology of the pest in relation to the environment and economic loss, with a view of separating aesthetic problems and those with cultural solutions from those with more genuine economic or basic ecological problems. Pest outbreaks fostered by mismanagement of the environment should be solved by instituting proper management procedures, e.g. weedy plant invasion of overgrazed pastures is best corrected by proper range management, such as reducing the number of cattle per acre, instituting a proper rotation schedule, etc.

Improved research on the ecology of both the pest and the proposed control organism will minimize the risks. The ecology of each organism proposed for importation should be worked out in the geographical areas where it already occurs in order to predict its range, habitat preferences, and any special problems before its introduction is attempted. Where classical biocontrol is shown to be the preferable method, it will pay to do the requisite ecological research to find the organism with the best potential for control which presents the least risk to non-target organisms and the environment. Historic introductions for biocontrol indicate that specialist species with narrow host ranges have been better control agents as well as having less impact on non-target organisms than have generalist species.

The current standard operating procedure of testing new importations in quarantine facilities against possible non-target organisms needs to be supported and expanded. Biocontrol agents should in principle not be introduced to control any native species. Considerable extra caution should be exercised on host specificity before any introductions to control species (e.g. Rubus spp.) closely related to native species are considered.

Research and assessment funds should be committed by the proposing agency at the time of introduction to support long-term assessment of the efficacy of the organism against the intended pest and its impacts on non-target organisms. Too many biocontrol "success" stories are based solely on hearsay.

A high priority is to work towards a consensus within the community on what constitutes a pest. We have endured enough of one public agency planting lantana (Lantana camara), melastomas, etc., as ornamentals along roadsides, in parks, and in public places, while another State agency introduces alien herbivores to control them. One State agency has imported alien predators in an attempt to reduce insect damage on haole koa, Leucaena leucocephala, while the national parks and many other land managers spend considerable money in an effort to control this alien weed. In most instances these short-term fixes are detrimental to native species. Let's give the natives a better chance by planning more for long-term solutions.

Conflicts also may arise even among researchers working towards control of pests impacting the native biota. For example, some of the biocontrol agents used against the mosquitoes that vector avian malaria and other diseases among native birds to date have disrupted native aquatic ecosystems and extirpated native species such as the damselfly Megalagrion pacificum. The early indications were that the koa psyllid Psylla uncatoides was a potential threat to both koa and the rare Acacia koaia and would compete with the native fauna associated with those trees; yet the introductions for biocontrol presented risks to some of the native psyllids and perhaps to other small, soft-bodied native foliar arthropods. These potential conflicts over what constitutes a pest and how to effectively deal with it, are best resolved with open review among concerned specialists and the public.

The most effective aegis for this open review is through the preparation of an environmental impact statement for proposed introductions. The history of environmental impacts by alien organisms demonstrates that the EIS process is justified. Persons who introduce animals or plants beyond their natural range undertake a grave responsibility. Society must discourage alien introductions in principle. Proposals for introductions must demonstrate convincingly that the new organisms will not harm the native flora or fauna, human health, or the local economy. Classical biocontrol has been shown to be largely irreversible and to have considerable environmental risks, and therefore should be used only as a last resort for legitimate serious pests. The hit-or-miss, shotgun approach of multiple species introductions espoused by earlier workers must end.

<u>Education</u>

A major factor for mitigating the negative impacts of alien species is education, and many educational recommendations were discussed under each of the above proposed solutions. Many pest problems actually involve only minor aesthetic damage or stem from the public's fear of the perplexing array of strange invertebrates. It is unfortunate that the advertizing and entertainment media prey on and reinforce a general phobia of insects and other "creepy-crawlies." If our educational system could overcome this cultural bias and instill a public appreciation of the aesthetics, right-to-life, interest, and importance of invertebrates in ecosystem functioning and human welfare, we would solve the majority of our "pest" problems.

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LITERATURE CITED

Beardsley, J.W. 1979. New immigrant insects in Hawaii: 1962 through 1976. Proc. Hawaii. Entomol. Soc. 23:35-44.

Beardsley, J.W. 1980. Haleakala National Park Crater District resources basic inventory: insects. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. 31. Honolulu: Univ. Hawaii.

Beardsley, J.W., and S. Fluker. 1967. Coptosoma xanthogramma (White), (Hemiptera: Plataspidae). Proc. Hawaii. Entomol. Soc. 19:367-72.

Bond, W., and P. Slingsby. 1984. Collapse of an ant-plant mutualism: the Argentine ant (Iridomyrmex humilis) and myrmecochorous Proteaceae. Ecology 65:1031-1037.

Carlquist, S. 1974. Island biology. New York: Columbia Univ. Pr.

Carson, H.L., and A.T. Ohta. 1981. Origin of the genetic basis of colonizing ability. In Evolution today: Proc. 2nd Internatl. Congr. Syst. Evol. Biol., ed. G.G.E. Scudder and J.L. Reveal, 365-370. Pittsburgh, Penn.: Hunt Inst. Bot. Doc., Carnegie-Mellon Univ.

Christensen, C.C. 1984. Are Euglandina and Gonaxis effective agents for biocontrol of the giant African snail in Hawaii? [Abstract] Am. Malacol. Bull. 2:98-99.

Clarke, B., J. Murray, and M.S. Johnson. 1984. Extinction of endemic species by a program of biological control. Pac. Sci. 38(2):97-104.

Conant, M. 1975. Seasonal abundance of the mamane moth, its nuclear polyhedrosis virus, and its parasites. U.S. Internatl. Biol. Prog. Island Ecosys. Tech. Rep. 64. Honolulu: Univ. Hawaii.

Connor, E.F., S.H. Faeth, D. Simberloff, and P.A. Opler. 1980. Taxonomic isolation and the accumulation of herbivorous insects: a comparison of introduced and native trees. Ecol. Entomol. 5:205-211.

Davis, C.J., and M. Chong. 1968. Recent introductions for biological control in Hawaii--XIII. Proc. Hawaii. Entomol. Soc. 20:25-34.

Donovan, B.J. 1980. Interactions between native and introduced bees in New Zealand. New Zealand J. Ecol. 3:104-116.

Fellers, J.H., and G.M. Fellers. 1983. Status and distribution of ants in the Crater District of Haleakala National Park. Pac. Sci. 36:427-437.

Gagne, W.C. 1971. Note on Xylosandrus compactus. Notes and exhibitions. Proc. Hawaii. Entomol. Soc. 21:19.

Gagne, W.C. 1979. Canopy-associated arthropods in Acacia koa and Metrosideros tree communities along an altitudinal transect on Hawaii Island. Pac. Insects 21(1):56-82.

Gagne, W.C. 1983. New invertebrate host associates of greensword. Notes and exhibitions. Proc. Hawaii. Entomol. Soc. 24:190.

Gagne, W.C., and F.G. Howarth. In press. Conservation status of endemic Hawaiian Lepidoptera. Proc. 2nd Europ. Lepidopt. Congr., ed. J. Heath.

Gerling, D. 1983. Nesting biology and flower relationships of Xylocopa sonorina Smith in Hawaii (Hymenoptera: Anthophoridae). Pan-Pac. Entomol. 58:336-351.

Goff, M.L. 1980a. Notes on Geckobiella sp. and Aponomma sp. Notes and exhibitions. Proc. Hawaii. Entomol. Soc. 23:175.

Goff, M.L. 1980b. Mites (Chelicerata: Acari) parasitic on birds in Hawaii Volcanoes National Park. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. 29. Honolulu: Univ. Hawaii.

Haas, R., and R. Pal. 1984. Mosquito larvivorous fishes. Bull. Entomol. Soc. Am. 30:17-25.

Hadfield, M.G., and B.S. Mountain. 1981. A field study of a vanishing species, Achatinella mustelina (Gastropoda, Pulmonata), in the Waianae Mountains of Oahu. Pac. Sci. 34(4):345-358.

Hara, H.H., and J.W. Beardsley. 1979. The biology of the black twig borer, Xylosandrus compactus (Eichhoff) in Hawaii. Proc. Hawaii. Entomol. Soc. 23:55-70.

Hardwick, D.F. 1965. The corn earworm complex. Entomol. Soc. Can. Mem. 40.

Hardy, D.E. 1981. Aneplolepis longipes (Jerdon). Notes and exhibitions. Proc. Hawaii. Entomol. Soc. 23:313.

Hardy, D.E., and M.D. Delfinado. 1974. Flightless Dolichopodidae (Diptera) in Hawaii. Proc. Hawaii. Entomol. Soc. 21:365-371.

Honegger, R.E. 1981. List of amphibians and reptiles either known or thought to have become extinct since 1600. Biol. Conserv. 19:141-158.

Howarth, F.G. 1983. Classical biocontrol: panacea or Pandora's box. Proc. Hawaii. Entomol. Soc. 24 (2&3):239-244.

Howarth, F.G., and J. Moore. 1983. The land nemertine Argonemertes dendyi (Dakin) in Hawaii (Nemertinea: Hoplonemertinea: Prosorhochmidae). Pac. Sci. 37:141-144.

Huddleston, E.W., and S.S. Fluker. 1968. Distribution of ant species of Hawaii. Proc. Hawaii. Entomol. Soc. 20:45-69.

Janzen, D.H. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day and insularity. Am. Nat. 54:687-708.

Klingman, D.L., and J.R. Coulson. 1983. Guidelines for introducing foreign organisms into the United States for the biocontrol of weeds. Bull. Entomol. Soc. Am. 29:55-61.

Leeper, J.R., and J.W. Beardsley. 1973. The bioecology of Psylla uncatoides in the Hawaii Volcanoes National Park and the Acacia koaia sanctuary. U.S. Internatl. Biol. Prog. Island Ecosys. Tech. Rep. 23. Honolulu: Univ. Hawaii.

Leeper, J.R., and J.W. Beardsley, Jr. 1977 [1976]. The biocontrol of Psylla uncatoides (Ferris and Klyver) (Homoptera: Psyllidae) on Hawaii. Proc. Hawaii. Entomol. Soc. 22:307-321.

Lewin, V., and J.C. Holmes. 1971. Helminths from exotic game birds of the Puu WaaWaa Ranch, Hawaii. Pac. Sci. 25:372-381.

Lubin, Y.D. 1984. Changes in the native fauna of the Galapagos Islands following invasion by the little fire ant, Wasmania auropunctata. In Evolution in the Galapagos, ed. R.J. Berry. London: Academic Pr.

Marshall, E. 1981. The summer of the gypsy moth. Science 213:991-993.

Mead, A.R. 1961. The giant African snail. Chicago: Univ. Chicago Pr.

Mead, A.R. 1979. Pulmonates. Vol. 2B, Economic malacology with particular reference to Achatina fulica. London: Academic Pr.

Moore, N.W., and W.C. Gagne. 1982. Megalagrion pacificum (McLachlan)--a preliminary study of the conservation requirements of an endangered species. Rep. Odon. Spec. Group 3. Gland, Switzerland: Internatl. Union Conserv. Nat. and Nat. Resour.

Mueller-Dombois, D., and F.G. Howarth. 1981. Niche and life-form integration in island communities. In Island ecosystems: biological organization in selected Hawaiian communities, ed. D. Mueller-Dombois, K.W. Bridges, and H.L. Carson, 337-354. Stroudsburg, Penn.: Hutchinson Ross Pub. Co.

Mueller-Dombois, D., K.W. Bridges, and H.L. Carson, eds. 1981. Island ecosystems: biological organization in selected Hawaiian communities. Stroudsburg, Penn: Hutchinson Ross Pub. Co.

Nakahara, L.M. 1980. Survey report on the yellow jackets, Vespula pensylvanica (Saussure) and Vespula vulgaris (L.) in Hawaii. Honolulu: Hawaii State Dep. Agric. Mimeo.

Perkins, R.C.L. 1913. Introduction. In Fauna Hawaiiensis, ed. D. Sharp, Vol. 1, xv-ccxxviii, pls. 1-16. Cambridge, England: The Univ. Pr.

Pimentel, D., C. Glenister, S. Fast, and D. Gallahan. In press. Environmental risks of biological pest controls. Oikos.

Pyle, R., M. Bentzien, and P. Opler. 1981. Insect conservation. Ann. Rev. Entomol. 26:233-258.

Ripperton, J.C., and E.Y. Hosaka. 1942. Vegetation zones of Hawaii. Hawaii Agric. Exp. Stn. Bull. 89.

Risch, S.J., and C.R. Carroll. 1982. The ecological role of ants in two Mexican agroecosystems. Oecologia (Berl.) 55:114-119.

Roubik, D.W. 1983. Experimental community studies: time-series tests of competition between African and neotropical bees. Ecology 64:971-978.

Roubik, D.W., and S.L. Buchman. 1984. Nectar selection by Melipona and Apis mellifera (Hymenoptera: Apidae) and the ecology of nectar intake by bee colonies in a tropical forest. Oecologia 61:1-10.

Schonewald-Cox, C.M. Genetics, minimum population size, and the island preserve. [This volume]

Severns, M. 1984. Another threat to Hawaii's endemics. Hawaii. Shell News 32(12):1, 9.

Solem, A. 1976. Endodontoid land snails from Pacific islands (Mollusca: Pulmonata: Sigmurethra). Part I: Family Endodontidae. Chicago: Field Mus. Nat. Hist.

Southwood, T.R.E. 1960. The abundance of the Hawaiian trees and the number of associated insect species. Proc. Hawaii. Entomol. Soc. 17:299-303.

Stein, J.D. 1983. The biology, host range, parasites, and hyperparasites of koa seed insects in Hawaii: a review. Proc. Hawaii. Entomol. Soc. 24:317-326.

Strong, D.R., Jr. 1979. Biogeographic dynamics of insect-host plant communities. Ann. Rev. Entomol. 24:89-119.

Swezey, O.H. 1931. Records of introduction of beneficial insects into the Hawaiian Islands. In Handbook of insects and other invertebrates of Hawaiian sugar cane fields, comp. F.X. Williams, 368-377. Honolulu: Hawaii Sugar Planters Assn.

Templeton, A.R. 1979. Genetics of colonization and establishment of exotic species. In Genetics in relation to insect management, ed. M.A. Hoy and J.J. McKelvey, Jr. Rockefeller Found. Conf., 31 March - 5 April, 1978. Gellagia, Italy: Rockefeller Found.

Tillier, S., and B.C. Clarke. 1983. Lutte biologique et destruction du patrimoine genetique; le cas des mollusques gasteropodes pulmones dans les territoires francais du Pacifique. Genet. Sel. Evol. 15(4):559-566.

Tomich, P.Q. 1969. Mammals in Hawaii. B.P. Bishop Mus. Spec. Pub. 57.

van der Schalie, H. 1969. Man meddles with nature - Hawaiian style. The Biologist 51(4):136-146.

van Riper, S., and C. van Riper III. A summary of known parasites and diseases recorded from the avifauna of the Hawaiian Islands. [This volume]

Wagner, W.L., D. Herbst, and R. Yee. Status of the native flowering plants of the Hawaiian Islands. [This volume]

Wells, S.M., R.M. Pyle, and N.M. Collins, comps. 1983. The IUCN Invertebrate Red Data Book. Gland, Switzerland: Internatl. Union Conserv. Nat. and Nat. Resour.

Zimmerman, E.C. 1948. Insects of Hawaii. Vol. 1, Introduction. Honolulu: Univ. Hawaii Pr.

Zimmerman, E.C. 1958. Insects of Hawaii. Vol. 7. Macrolepidoptera. Honolulu: Univ. Hawaii Pr.

IMPACT OF ALIEN PLANTS ON HAWAI'I'S NATIVE BIOTA

Clifford W. Smith

ABSTRACT

Over 4,600 species of plants have been introduced into the Hawaiian Islands over the last 200 years. Only 86, less than 2% of the total, have become serious pests of native ecosystems. Of these, the most significant are Andropogon virginicus, Clidemia hirta, Lantana camara, Leucaena leucocephala, Melinis minutiflora, Myrica faya, Passiflora mollissima, Pennisetum clandestinum, P. setaceum, Psidium cattleianum, Rubus argutus, and Schinus terebinthifolius. All 86 species are discussed with regard to their impact on the ecosystem, dispersal mechanism, fire tolerance, potential for biological control, and their distribution and principal infestation sites. Twenty-eight (32%) are invasive weeds; the remainder generally require some form of disturbance in order to become established.

The lowland ecosystems have suffered the most disruption from alien species because of agriculture, fire, and urbanization. However, all vegetation types have been affected to some degree. The ecosystems least impacted are alpine habitats, rain forests, and bogs, although they are coming under increasing pressure.

A number of strategies are discussed which may help to ameliorate weed problems. Greater effort by government is needed to educate the public on the need for importation control and to enforce regulations. Mechanical and herbicidal control is discounted except in small areas. Biological controls offer considerable hope, but there are many problems associated with this strategy.

The unique flora and fauna of the Hawaiian Islands is seriously threatened by alien plants. Many native species have already been extirpated. Unless importation of aliens and the continuing disturbance of the

native ecosystems is stopped, the prognosis for the remaining native biota is grim.

INTRODUCTION

"The history of weeds is the history of man" (Anderson 1952); the development of the Hawaiian flora is a classical example. Prior to the colonization of the Hawaiian Islands by man, the rate of introduction of plants was very low because of difficulties of dispersal over 3,200 km of ocean and subsequent establishment. The approximately 272 plants that did become established adapted and diversified to produce a flora of 1,729 species and varieties, 95% of which are endemic (Fosberg 1948). The aboriginal Hawaiians accelerated the process of introduction by bringing with them plants necessary for their culture. These plants had a distinct advantage in the process of establishment because they were deliberately cultivated. Most were cultivars and less than 25 escaped, but St. John (1978) listed 7 additional weeds which he believed were introduced inadvertently. The major impact of the Hawaiians was restricted to the lowlands, resulting from the clearing and burning of the native vegetation (Kirch 1982).

On the arrival of Captain Cook in 1778, the rate of plant introductions increased. Each new culture arrived with plants necessary for their cuisine or pleasure. Agricultural interests accelerated the process even more by bringing in pasture grasses and forb seeds which generally were contaminated with weeds from other sources, a common problem until quite recently (Salisbury 1964). Finally, foresters brought in trees, initially to reforest watershed areas devastated by feral cattle (Bos taurus), but later to establish a forestry industry in the Islands. Introductions of horticultural interest continue even today with little control except for a specific ban on a number of drug-producing plants and officially declared "noxious" weeds. Statutes exist which regulate the importation of plants, but they are only cursorily enforced except for those plants that come in under permit. The State's overriding concern is to protect and promote agricultural and other economically attractive interests, and protection of native ecosystems has received little consideration.

There are over 4,600 alien species in Hawaii (St. John 1973), of which over 600 have become naturalized (W.L. Wagner, pers. comm.). In this paper 86 are considered pests in areas not cultivated or urbanized. Many other weeds are confined to agricultural areas (Haselwood and Motter 1983). Although the term "pest" normally connotes social, economic, and biological problems (Norton and Conway 1977), in this paper it is used solely in the context of a weed's disruptive impact on the natural processes of native ecosystems. Species that prevent the reestablishment of native communities are included, along with those which invade disturbed or undisturbed native communities. Several species that may be considered beneficial by agronomists or horticulturists as forage, ornamentals, or for timber are included in this listing because of their negative impact in native Hawaiian ecosystems.

TERMINOLOGY

Six terms (adventive, alien, exotic, introduced, naturalized, and weed) are commonly used to describe species not native to an area. In Hawai'i most people use "exotic" and "introduced", or more rarely "adventive". It may seem overly critical to worry about which term is correct. However, we are discussing not only a problem of communication among scientists, but also with the general public. The semantic confusion, particularly for the non-scientist, could prevent understanding of some essential elements of the problem. The term "exotic", although literally correct, is inappropriate because it also implies something excitingly different. "Adventive" is a word with a specific botanical meaning, i.e., not native to the environment, but it is generally used to refer to accidental introductions which persist for a while and then disappear. It is also somewhat indiscriminate in that it can be used to refer to a species introduced from a neighboring ecosystem. "Introduced" is probably appropriate except that it implies a deliberate action and does not carry the negative implication of the term "alien." The term "naturalized" is unsuitable because it refers to alien species which have become established and self-sustaining in a new geographic area. Not all alien species are naturalized and not all naturalized species are pests.

In many parts of the world, "alien" is the preferred word. "Alien" is appropriate because its meaning is direct and it also has the connotation of not belonging, a strongly desirable implication. The term "weed" refers to the functional role of an organism and is inappropriate in this context because not all alien plants are weeds and native species can also be weeds. Two endemic species, *Cuscuta sandwiciana* Choisy (dodder) and *Hesperocnide sandwicensis* Wedd. (stinging nettle), have been declared noxious weeds by the State of Hawai'i, and an additional 7 endemic and 8 indigenous species have been called weeds (Haselwood and Motter 1983; Hosaka and Thistle 1954). The word alien will be used in this paper and its use is encouraged elsewhere.

Acacia mearnsii Willd. (A. decurrens (Wendl.) Willd. in Hawaiian literature) (Black wattle)

This noxious, evergreen tree often reaches 20 m in height. Apart from producing copious numbers of seeds, it generates numerous suckers resulting in monotypic thickets. The small seeds are not actively dispersed and, although rodents or granivorous birds cannot be totally discounted, man appears to be the principal disseminator. The species resprouts by basal shoots following fire, thereby generally intensifying the infestation. No evaluation of its potential for biological control has been made.

It grows in disturbed, mesic habitats between 600-1,700 m. The major infestation is at Kula, Maui.

Acacia confusa Merr. (Formosan koa)

This evergreen tree is prized by many for its brilliant display of bright yellow, mimosoid flowers and its ability to grow in poor, dry soils. It reaches heights of 15 m and shades out most other plants. The small seeds are passively dispersed. Man has been the principal disseminator through aerial broadcasting. The leaves are apparently allelopathic since the ground underneath these trees is barren except for a few alien weeds, e.g., Stachytarpheta jamaicensis (L.) Vahl (Jamaica vervain). The plant is essentially fire resistant because fire will not carry under the tree due to the lack of fuel. Aerial portions which are only scorched will resprout rapidly. No evaluation of potential for biological control has been made.

It thrives between sea level and 700 m elevation in dry and mesic habitats. Major infestations are found on the windward side and Wai'anae Mountains, O'ahu, and the north shore of East Maui.

Acacia farnesiana (L.) Willd. (Klu, popinac)

This thorny, deciduous shrub grows to 4 m in height, sometimes forming impenetrable thickets, although in most areas it forms a more open cover. The seeds are dispersed by ungulates which eat the pods. Although the aerial portions may be killed by fire, it soon regenerates from basal shoots. It has not been evaluated for biological control.

Acacia grows in dry habitats between sea level and 1,000 m on all islands. There are some dense infestations at Lualualei, O'ahu, and Lihau, Maui; some overgrazed areas on Lana'i; and the Ha'upu area of Kaua'i, particularly Mahalapu.

Albizia falcataria (L.) Fosb. (Molucca albizia)

This elegant, deciduous tree with wide-spreading branches is used as a shade plant for coffee in many parts of the world. It grows very rapidly even on nutrient-poor soils. It is not known how the large seeds are dispersed, although man was initially the principal disseminator when seeds were sown from aircraft. It is not susceptible to control by fire because the trees are rarely subjected to fires of sufficient intensity. The potential for biological control has not been evaluated.

It grows from sea level to 1,500 m elevation but is most common in mesic, lowland areas. It is common in windward O'ahu, in the Mililani area and above Lualualei, O'ahu, and in upper Wailua, Kaua'i. It is still planted as an ornamental and in forest plantations in Hawai'i.

Andropogon glomeratus (Walt.) BSP. (Bush beardgrass)

The problems associated with this species and its ecological preferences are the same as A. virginicus. It is confined to the island of Hawai'i.

Andropogon virginicus L. (Broomsedge)

This perennial bunchgrass sometimes forms continuous cover in boggy, open mesic and dry habitats. It releases highly persistent allelopathic substances (Rice 1972). The dead material provides an excellent fuel for fires. It is fire-stimulated; its cover increases dramatically with each fire (Smith, Parman, and Wampler 1980). In areas where it occurs, both fire intensities and acreage burnt have increased. Because it retains the phenology of its native habitat, the southeastern United States, its growth is out of synchrony with Hawai'i's climatic pattern (Sorensen 1980). It is dormant during the rainy season, which Mueller-Dombois (1973) has shown leads to increased erosion in some areas. The seeds are dispersed by wind. The potential for biological control has been discussed by Gardner and Davis (1982), but attempts to evaluate possible agents in Hawai'i probably will be resisted by the sugar industry.

It is widely distributed from sea level to at least 1,600 m on all major islands. Major infestations occur on the windward plain and Pupukea areas of O'ahu, overgrazed ridges in East Moloka'i, and the Puna and Ka'u regions of Hawai'i.

Anthoxanthum odoratum L. (Sweet vernalgrass)

This small, perennial bunchgrass forms extensive ground cover in open mesic and dry habitats at high elevations. It invades disturbed areas, preventing the reestablishment of native species. The seeds are dispersed by wind. Its cover increases after fire, but this increase appears to be the result of reduced competition rather than stimulation. It has not been evaluated for biological control.

It occurs between 1,500-3,000 m on Haleakala, Maui, and Mauna Kea and Mauna Loa, Hawai'i. Some scrubland habitats on Haleakala have almost pure stands of this grass between the bushes.

Ardisia humilis Vahl (Shoebutton ardisia)
This shade-tolerant, evergreen tree grows rapidly, forming dense monotypic stands that prevent establishment of all other species. Alien frugivorous birds are the principal dispersal agent. The red-vented bulbul (Pycnonotus cafer) is attracted to its numerous red to blackish fruit. It will be interesting to note the impact of this recently established frugivorous bird on the distribution and infestation levels of this tree on O'ahu. The tree is probably not resistant to fire, and the potential for biological control has not yet been evaluated.

The species is confined to wet, lowland areas. The principal infestations are Waikane-Waiahole, O'ahu and Hana, Maui.

Asystasia gangetica (L.) Anders. (Chinese violet)
Chinese violet is a rapidly growing perennial, shrubby herb which grows to 1 m height but can grow over shrubs up to 3 m tall. It can smother all vegetation in the herbaceous layer. The seeds are dispersed from explosive capsules but long-distance dispersal is effected by man. Although aerial portions may be killed by fire, the plant soon regenerates from basal shoots or seeds. It has not been evaluated for biological control.

Chinese violet grows in dry habitats between sea level and 300 m on all islands. There are dense infestations at Lualualei, 'Ewa Plains, Diamond Head, and Koko Head, O'ahu.

Bambusa sp. (Bamboo)
This large bamboo forms extensive, impenetrable thickets. It spreads into adjacent areas, overshadowing all but the tallest trees. The species has not yet reproduced in Hawai'i, so we do not know whether it will set viable seed. Fires rarely carry through stands because of the lack of sufficient fuel. Though aerial shoots at the edge of the colony are destroyed by fire, the stand recovers rapidly by means of subterranean shoots. Since the species name is not known with certainty and it is a useful plant to many, it has not been evaluated for biological control.

There are major infestations in the northern valleys of Kaua'i, e.g., Limahuli Valley, the forests above Honolulu from 'Aiea to Niu and from Kailua to Kipahulu, Maui. It is confined to elevations below 400 m.

Bidens pilosa L. (Beggar's tick)

This annual to almost perennial shrubby herb forms dense cover along roads, trails and open lowland areas. It is dispersed on human clothing and animal coats. It is not fire tolerant but quickly invades burnt areas. Biological control of this species could be complicated by the presence of endemic species in this genus.

The plant is widely distributed and common in open areas up to 1,300 m. There are several areas on the south slope of Haleakala and the central valley of Maui where carpets of this species inhibit the establishment of native species during the rainy season.

Bocconia frutescens L.

This evergreen shrub to small tree forms dense stands in dry habitats. The seeds are wind-dispersed. Its fire tolerance in Hawai'i is unknown. It has not been evaluated for biological control.

It grows at elevations between 300-1,000 m in dry habitats on Maui and Hawai'i. There is a significant infestation above 'Ulupalakua, Maui.

Brachiaria mutica (Forsk.) Stapf (California grass)

This perennial grass can reach heights of 2 m. It forms dense monotypic stands by layering from trailing stems. It will overgrow most shrubs and trees in its habitat. It has mild allelopathic activity (Chou and Young 1975). Man is the principal dispersal agent. Fire is rare in its habitat but the dense stands rapidly regenerate from any damage that they suffer. It has not been evaluated for biological control because it is a valued pasture grass in lowland areas.

The species grows in wet habitats between sea level and 700 m. Open marshy areas, such as Kawainui Swamp, O'ahu, are the principal habitat.

Brassaia actinophylla Endl. (Octopus tree)

This fast-growing, evergreen tree with few branches reaches heights of 15 m. It is a shade-tolerant plant capable of invading undisturbed forests. The seeds are dispersed by alien frugivorous birds. It is not tolerant of fire. It has not been evaluated for biological control.

It grows up to 1,000 m elevation in wet lowland habitats on all islands. There are major infestations in the northern valleys of Kaua'i, particularly Limahuli Valley, and in Nu'uanu and Waiahole Valleys, O'ahu.

Caesalpinia sepiaria Roxb. (Cats claw, Mysore thorn)

This deciduous, sprawling, noxious shrub, with numerous spines, forms impenetrable thickets. The medium-sized seeds may be dispersed by rodents and granivorous birds, but man is almost certainly the principal dispersal agent in Hawai'i. Fire tolerance in Hawai'i is unknown, and the potential for biological control has not been evaluated.

The plant is confined to dry to mesic lowland habitats. There are several infestations along the Honouliuli trail of the Wai'anae Mountains and on the windward side of O'ahu, the upper pastures and adjacent forest of much of northeastern Kaua'i, and Kakipi Gulch, Maui.

Casuarina equisetifolia Stickm. (Common ironwood)

This rapidly growing tree can reach heights of 40 m or more. It forms monotypic stands under which little else grows. The lack of undergrowth beneath trees suggests the release of an allelopathic agent, although Neal (1965) suggested that it exhausts the nutrients in the soil. The seeds are wind-dispersed. The lack of undergrowth prevents very hot fires from burning in the vicinity of these trees. When fires do sweep through stands, trees regenerate rapidly from basal shoots. The species has not been evaluated for biological control because it is still considered a beneficial tree for windbreaks, erosion control, and nitrogen fixation.

It is common in all but the driest and wettest coastal areas of all islands up to 500 m.

Casuarina glauca Sieb. in Spreng. (Swamp oak)

This species is very similar to C. equisetifolia. However, it forms suckers prolifically, producing dense stands. It is the most aggressive ironwood in the Islands.

It has a similar distribution to C. equisetifolia.

Cecropia peltata Sandmark (Trumpet tree)

This very rapidly growing but short-lived tree attains a height of no more than 10 m. It forms dense stands which seriously impede the growth of other plants. The seeds are dispersed by alien frugivorous birds. It is destroyed by fire and has not been evaluated for biological control.

It grows in wet lowland habitats of all major islands, but there is a major infestation in Manoa Valley, O'ahu, and the Waiakea area, Hawai'i.

Cenchrus ciliaris L. (Buffelgrass)

This small, perennial bunchgrass forms continuous cover in arid habitats. The dried shoots provide an excellent fuel for fire, from which the plant recovers rapidly by basal shoots. It is a fire-enhanced species as its cover increases with each succeeding fire. The seeds are dispersed by wind. It has not been evaluated for biological control, because of its extensive use in erosion control.

The species is confined to arid habitats between sea level and 150 m elevation. There are major infestations at Lualualei, O'ahu; Kihei, Maui; on Kaho'olawe; and at Kawaihae, Hawai'i. It has recently become the dominant grass on Molokini Island.

Citharexylum caudatum L. (Juniper berry)

This evergreen shrub to small tree forms dense thickets in wet habitats. It has many characteristics in common with C. spinosum.

It recently escaped from the Lyon Arboretum in Manoa Valley, O'ahu and has since moved rapidly into the Ko'olau Mountains in that region.

Citharexylum spinosum L. (Fiddlewood)

This evergreen, medium-sized tree does not have the spines that its scientific name suggests. It forms crowded stands even in undisturbed habitats and is dispersed by alien frugivorous birds. Its fire response in Hawai'i is unknown. It has not been evaluated for biological control.

The tree has escaped only recently and is a pest only on O'ahu. Gerrish and Mueller-Dombois (1980) describe 2 infestations at Tantalus and Pupukea. However, extensive use as an ornamental by landscapers on other islands will result in infestations there also.

It grows in wet habitats generally below 500 m. There is a population at the bottom of the cliffs in Waimanalo in a very dry habitat. This population is deciduous during the dry season, and it can be seen from a considerable distance when the leaves turn red prior to fall.

Clerodendron japonicum (Thunb.) Sweet (Glorybower)

This ornamental shrub has escaped on Kaua'i in the Oma'o area, where it is becoming a serious pest. It has recently escaped in Wailau Valley, Moloka'i. The fruit is dispersed by alien frugivorous birds. Its susceptibility to fire is not known, and it has not been evaluated for biological control.

Clidemia hirta (L.) D. Don (Koster's curse)

This noxious weedy shrub grows up to 2 m tall in pastures and forest. It is an aggressive invader which shades out all vegetation below it (Wester and Wood 1977). The seeds are principally dispersed by alien frugivorous birds, but any organism moving through the thickets will carry seeds away with it. It is probably not resistant to fire, an unlikely event in its habitat, but it rapidly colonizes burned areas. Several expeditions for potential biological control agents have been made in Trinidad, and a number of insects are being screened currently.

This plant is a serious pest in mesic and wet environments on O'ahu and more recently in Wailau, Moloka'i, as well as Nahiku and Kailua areas, Maui. It has also become established on Kaua'i, West Maui, and Waiakea, Hawai'i. There is increasing evidence that many of the new infestations are inadvertently established by marijuana growers.

Corynocarpus laevigatus J.R. & G. Forst. (New Zealand laurel)

This evergreen tree reaches heights of 15 m. It forms a dense shade excluding other species. The fruit, which is very poisonous to man, is dispersed by alien frugivorous birds. Its fire tolerance is unknown, and it has not been evaluated for biological control.

It grows in mesic habitats between 700-1,500 m. There is a major infestation in Koke'e, Kaua'i.

Eugenia cumini (L.) Druce (Java plum)

This large evergreen tree forms a dense cover, excluding all other species. The large black fruit are dispersed by alien frugivorous birds and perhaps occasionally by feral pigs (Sus scrofa). Although it is not an aggressive invader of undisturbed forest like the closely related roseapple, it prevents the reestablishment of native lowland forest. It is not really fire resistant, but fires are rarely intense enough in the stands to produce other than peripheral damage. This tree has not been evaluated for biological control.

It is found in dry to mesic and more rarely wet lowland areas up to 700 m on all major islands. There is a heavy infestation at Kalalau Valley, Kaua'i, and Kalaupapa, Moloka'i.

Eugenia jambos L. (Roseapple)

This medium-sized deciduous tree forms dense thickets which shade out native species. It invades undisturbed forest. The fruit is dispersed by humans and perhaps feral pigs. It is not known to be fire resistant. It has not been evaluated for biological control.

It is found in wet lowland habitats up to about 500 m elevation on most major islands. There is a major infestation in the Manuka Natural Area Reserve on Hawai'i.

Ficus microcarpa L.f. (Chinese banyan)

This evergreen tree produces a very dense shade excluding all other species. It does not invade undisturbed forest but once established it will displace all other trees in its shade. The fruit are dispersed by alien frugivorous birds. Although it is susceptible to fire, it is only marginally affected because fire will not carry under the tree for lack of fuel. It has not been evaluated for biological control. There are a number of insects which attack it, most notably the Cuban laurel thrip (Gynaikothrips ficorum), but they do not reduce the vigor of most trees.

This species grows in all but the wettest and driest habitats on all of the major islands, most commonly on cliffs and rocky outcrops. It has the potential to grow up to 1,500 m but rarely grows much above 700 m. There are some particularly large trees along the Hana coastline, Maui.

Fraxinus uhdei (Wenzig) Lingelsheim (Mexican ash)

This tall, deciduous tree has been planted extensively by foresters. It is among the most successful trees for reforestation and has spread into adjacent areas, forming dense stands from which most native species are excluded. The seeds are dispersed by wind. Its response to fire in Hawai'i is unknown. Because of its use in forestry, it is very unlikely that it will be evaluated for biological control.

The most extensive infestations are along the Honouliuli trail, O'ahu; on Moloka'i; and in the Makawao Forest Reserve and Olinda areas, Maui. It grows best between 1,000 and 1,750 m but also grows up to 2,000 m.

Furcraea foetida (L.) Haw. (Mauritius hemp)

This large, rosette plant rarely grows above 1.5 m though the inflorescence may reach 5 m. The inflorescence produces bulbils rather than seeds which are dispersed locally, forming dense monotypic thickets. The plants are not susceptible to fire, which does not move through concentrations of this plant. It has not been evaluated for biological control.

This plant grows between sea level and 1,000 m in dry habitats. There are major infestations along the Napali coast, Kaua'i, and near Wailuku, Maui.

Grevillea banksii R. Br (Kahili flower)

This noxious, medium-sized, evergreen tree is similar to silky oak in most features. There is a major infestation in the Ka'u District, Hawai'i.

Grevillea robusta A. Cunn. in R. Br. (Silky oak)

This large, evergreen tree has been used extensively in reforestation programs. The leaves produce an allelopathic substance which inhibits the establishment of all species, including itself. The seeds are wind-dispersed, and adaptation to fire in Hawai'i is unknown. Because of its use in forestry and as a shade tree by some ranchers, it has not been evaluated for biological control.

It is quite widespread in dry areas between 350-1,600 m elevation on all major islands.

Hedychium coronarium Koenig (White ginger)

The problems with this fragrant-flowered species are very similar to those for H. gardnerianum. However, reproduction by seeds, which are not produced in large numbers, is localized because they are rarely displayed conspicuously. Long-distance dispersal is effected vegetatively by man. Its adapatation to fire is unknown but unless the fire is intense enough to harm the rhizomes it will recover. The potential for biological control is poor because of the extensive use of this species in gardens and lei making.

This species is widely distributed in wet habitats on all islands. There are major infestations in Nahiku, Maui; and Puna and Kohala Mountains, Hawai'i.

Hedychium flavescens Carey in Roscoe (Yellow ginger)

The problems associated with this species are identical to those of H. coronarium.

This species is very common in the wetter northern valleys of Kaua'i but is also found in many of the same habitats as the white ginger.

Hedychium gardnerianum Roscoe (Kahili ginger)

This showy ginger grows just over 1 m tall. Each plant grows rapidly by stolons, displacing all other plants. The conspicuous, fleshy, red seeds are dispersed by alien, and perhaps native, frugivorous birds as well as man. Adaptation to fire is unknown, but unless the fire is intense enough to harm the rhizomes, it will recover. Gardner and Davis (1982) discussed the potential for biological control of this species but noted the almost certain opposition from horticulturists to any move in this direction.

The plant grows in wet habitats on all islands between sea level and 1,700 m. There are major infestations at Koke'e, Kaua'i; Nahiku, Maui; and Volcano, Hawai'i.

Heliocarpus popayanensis HBK. (White moho)

This tall tree, planted extensively by foresters, has escaped into wet forests at low to mid elevations. The seeds are dispersed by wind. Its response to fire is unknown, and it has not been evaluated for biological control.

There are some potentially troublesome infestations at the base of Kaua in the Wai'anae Mountains, and Manoa Valley, O'ahu, as well as Mountain View, Hawai'i.

Holcus lanatus L. (Velvetgrass)

This perennial bunchgrass invades disturbed sites rapidly. It forms dense stands which shade out seedling establishment, but allelopathic activity is also suspected (Watt 1978). Seeds are produced abundantly and dispersed by wind. Seedling growth is much more rapid than in native species. As with most bunchgrasses, this species tolerates fires and regenerates rapidly from basal shoots. Holcus has not been evaluated for biological control but potential agents and the effectiveness of some herbicides are noted by Watt (1978). The sugar industry will probably resist any move to import biocontrol agents.

This plant is widely distributed in all but the most xeric habitats above 1,300 m. Jacobi (1981) suggested that, once disturbance is eliminated, Holcus will remain stable in a native grassland community.

Hypochoeris radicata L. (Hairy cats-ear)

This small rosette herb is very common above 2,000 m on Maui and Hawai'i. It has a deep, succulent taproot favored by feral pigs, which dig up large areas searching for the roots. Seeds are produced in large numbers and dispersed by wind. It regenerates rapidly from the crown of the taproot after fire. It has not been evaluated for biological control.

Lantana camara L. (Lantana)

This thorny shrub is a noxious weed. It can form impenetrable thickets which crowd out other plants. The fruit are dispersed by alien frugivorous birds. It is capable of surviving all but the hottest fires, regenerating from basal shoots. Allelopathic substances are produced by shoots and roots (Achhereddy and Singh, in press). The plant has been subjected to biological control which has been quite effective in some areas (Gardner and Davis 1982). Further control agents are being sought.

Lantana is found up to 600 m on all islands, principally in dry areas. It has infested both mesic and wet habitats as well.

Leptospermum ericoides A. Rich. (Tree manuba)

This tree is similar to L. scoparium. It is confined to Lana'i.

Leptospermum scoparium J.R. & G. Forst. (New Zealand tea)

This small, scrubby tree forms thickets which crowd out other plants. On Lana'i, it has infested goat (Capra hircus)-eroded ridgetops, resulting in their stabilization. It appears to have allelopathic activity like many other members of the Myrtaceae. The seeds are dispersed by wind. Its response to fire in Hawai'i has not been established, nor has it been evaluated for biological control.

It is found in mesic habitats between 300-700 m elevation. The principal infestations are on Lana'i and above La'ie in the Ko'olau Mountains, O'ahu.

Leucaena leucocephala (Lam.) de Wit (Koa haole)

This thornless tree forms dense thickets, excluding all other plants. It is grown for fodder, but unless severely grazed or controlled, it spreads rampantly throughout adjacent areas. The seeds are not actively dispersed except occasionally by rodents and alien granivorous birds. It regenerates rapidly from basal shoots after fire. There is also a flush of new seedlings produced following fire, but whether this is the result of normal germination or breaking dormancy by fire is not known. In mature monotypic stands fire is suppressed because of the low fuel load. The potential for biological control has been evaluated by Gardner and Davis (1982), but no action is likely to be taken because of its use in agriculture and use of closely related species as fuel crops. In fact, the State Department of Agriculture may import parasites of the recently introduced Heteropsylla cf. incisa (Nakahara and Lai 1984) which has considerable potential as a control agent of koa haole.

Koa haole is found in dry to mesic habitats on all islands up to 700 m, having been deliberately broadcast over lowland habitats approximately 50 years ago. It is also present in severely disturbed wet areas but not as a dominant species.

Linociera intermedia Wight (Olive) (? = L. ligustrina)

This shrubby, evergreen tree forms dense, monotypic thickets between 500-1500 m elevation. It may have allelopathic activity. The seeds are dispersed by alien frugivorous birds. Its adaptation to fire is unknown, and it has not been evaluated for biological control.

The major infestations are at Waimea, Hawai'i and 'Ainahou, Hawai'i Volcanoes National Park.

Melaleuca leucadendra (Stickm.) L. (Paperbark)

This evergreen tree reaches heights of 12 m and has been planted extensively in reforestation projects. It invades open swampy areas. The leaves appear to have allelopathic activity, probably of a similar nature to that of other members of the Myrtaceae. The seeds are dispersed by wind. Like many other members of its family, it is adapted to fire, which generally results in an intensification of the infestation. It has not been evaluated for biological control.

Paperbark infests wet habitats between 100-1,000 m. The principal infestations are above Kalaheo, Kaua'i; in the Ko'olau Mountains, O'ahu; and in the Metrosideros dieback area on the north slope of Haleakala, Maui.

Melastoma malabathricum L. (Indian rhododendron)

This noxious, spreading shrub forms tangled brush up to 2 m tall which crowds out all other species. Its berry-like fruit is dispersed by frugivorous birds. There is no information on its adaptation to fire. Although Gardner and Davis (1982) suggested that it has been partially controlled by Selca brunella Hampson caterpillars, there is little evidence of any decrease in population levels.

There are heavy infestations on Kaua'i and the Puna and Hamakua Districts of Hawai'i from sea level to 700 m. In some areas of Kaua'i, particularly in Kilohana Crater, it is being replaced by Rhodomyrtus tomentosa.

Melia azedarach L. (Pride of India)

This fast-growing, deciduous tree reaches 20 m in height. Its wide-spreading branches form a deep shade. There does not appear to be a natural seed dispersal agent present in the Islands; it is thought that man is responsible for dispersal. Adaptation to fire in Hawai'i is unknown, and it has not been evaluated for biological control.

It grows between sea level and 700 m in open dry habitats. There are major infestations in Waimea Canyon, Kaua'i; Nu'u and lower Kula, Maui; and Kona, Hawai'i.

Melinis minutiflora Beauv. (Molassesgrass)

This spreading, perennial mat grass smothers everything around it. Once established, it forms monotypic stands from rooted runners. It is considered a good forage grass and therefore is not a candidate for biological control. The seeds are dispersed by wind. It is adapted to fire, and the dense mats are generally only partly consumed. Regeneration from the remaining portions is rapid, and colony expansion into adjacent burned areas generally follows.

It is found on all islands from sea level to 1,500 m in dry and mesic environments.

Melochia umbellata (Houtt.) Stapf. (Melochia)

This small, fast-growing, shrubby tree was originally introduced to produce shade for young forest trees and perhaps coffee. It rapidly fills any available space after disturbance, displacing the slower growing native species. The seeds are dispersed by wind. Adaptation to fire is unknown, and it has not been evaluated for biological control.

The major infestations are in Puna and Hilo, Hawai'i.

Merremia tuberosa (L.) Rendle (Woodrose)

This light-loving, perennial vine can smother tall forest canopies. The seeds are almost exclusively distributed by man, who introduces it to new areas principally as a source of material for dried flower arrangements. The aerial portion of the plant is killed by fire, but a new vine is soon produced from its underground tuber. It has not been evaluated for biological control.

Woodrose grows in open mesic forests from sea level to 1,400 m. Many areas of Kaua'i are infested, e.g., Puhi, west of Lihu'e.

Miconia magnifica (Triana)

This evergreen tree escaped from a local garden very recently. It forms densely shaded, monotypic stands. We know little about its local biology but anticipate that it will have the same impact in Hawai'i as it has had in Tahiti, where it has rapidly invaded native forests with disastrous consequences for the native flora. Its adaptation to fire is not known, and it has not been evaluated for biological control.

There is a population established in the Hilo area which should be eliminated immediately. Unfortunately, it is still being sold by garden shops. The species should be classified as noxious.

Microlaena stipioides (Labill.) R. Br. (Meadow rice-grass)

This wiry, perennial tufted grass is common in moist and wet habitats. It invades disturbed sites rapidly. The awned fruit are dispersed on clothing or animal fur. It is a fire-stimulated grass and in Hawai'i carries fires over larger areas than normal. It has not been evaluated for biological control.

It grows between 100-1,500 m in dry to mesic areas. There are major infestations from Puna to South Kona on Hawai'i.

Myrica faya Ait. (Fayatree, firetree)

This rapidly growing, noxious, evergreen tree, reaching up to 15 m in height, invades mesic and wet habitats where it forms dense, monotypic stands. The leaves are suspected of some allelopathic activity. The fruit is dispersed by alien and native frugivorous birds (La Rosa 1983) and feral pigs (C. Stone, pers. comm.). Trees are normally killed by fire, although regeneration from basal sprouts is possible. It has been and still is being evaluated for biological control (Gardner and Davis 1982). Exploration for potential biological control agents was made in 1984.

Myrica grows between 300-1,700 m elevation. The principal infestations are in Koke'e, Kaua'i; Wai'anae Mts., O'ahu; lower Kula, Maui; Ko'ele, Lana'i; and Hamakua, Hualalai, and Volcano Golf Course and Hawai'i Volcanoes National Park, Hawai'i.

Panicum maximum Jacq. (Guinea grass)

This coarse, perennial grass reaches heights of more than 2 m. It has a strong allelopathic activity (Chou and Young 1975). The seeds are dispersed by wind, and it can survive long periods of drought. Fire will sweep through stands of this grass but it regenerates rapidly from underground rhizomes. It has not been evaluated for biological control.

It grows in dry areas between sea level and 1,200 m on all major islands.

Paspalum conjugatum Berg. (Hilo grass)

This perennial, stoloniferous grass rapidly invades wet habitats from sea level to 2,000 m. It forms a dense ground cover even on acidic, low-nutrient soils. Neal (1965) noted that "some native forests have become extinct due to this pest." The small seeds are probably distributed by man and animals on clothing and fur. This species is generally susceptible to fire, an unlikely event in the rain forest. No serious effort has been made to evaluate this pest of native ecosystems and ranchlands for biological control.

It is found in wet habitats on all islands.

Passiflora ligularis Juss. (Sweet granadilla)

This vine is a weed with many similarities to P. mollissima. The major infestation is at Ka'upulehu, Hualalai, Hawai'i.

Passiflora mollissima (HBK.) Bailey (Banana poka)

This light-loving vine can rapidly reach and smother the forest canopy when the sub-canopy vegetation is disturbed either naturally, by hurricanes and other high winds, or by man or feral pigs (La Rosa 1983). Feral pigs are the principal short-distance dispersal agents (Warshauer et al. 1983). Alien frugivorous and granivorous birds as well as man act as long distance dispersal agents. Adaptation to fire is not known. This pest is the subject of an exploration for biological control agents supported by the State Department of Land and Natural Resources (DLNR). Studies on the biocontrol potential of Fusarium oxysporum f. sp. passiflorae are in progress.

There are 3 major infestations on Hawai'i at Hualalai, Laupahoehoe, and Volcano, and another on Kaua'i at Koke'e (Warshauer et al. 1983). A population at upper Waiakoa, Maui, which had been thought to be eradicated has recently been relocated in several adjacent gullies.

Passiflora suberosa L. (Huehue-haole)

This vine does best in the subcanopy layers where it smothers shrubs, small trees and the ground layer. In some areas it also smothers the upper canopy layer. The seeds are dispersed by alien frugivorous birds. Adaptation to fire is not known, and it has not been evaluated for biological control.

This passionfruit is found in dryland habitats on all islands between sea level and 600 m. There are major infestations throughout the Wai'anae Mountains, O'ahu and along the Kahoma Ditch trail, Maui.

Pennisetum clandestinum Hochst. ex Chiov. (Kikuyugrass)

This rapidly growing, partially scrambling, rhizomatous plant is a favored, but overrated, rangeland grass. It is a serious pest in forests because, apart from shading out shrubs and herbs, it releases allelopathic substances which kill almost all other species in the vicinity (Sanchez and Davis 1969). It burns very slowly and generally retards fire. It has been evaluated for biological control but no action will be taken because of its agricultural importance (Gardner and Davis 1982). A rust (Phakospora apoda (Har. and Pat.) Mains) has recently become established on all islands but its impact is not yet known (Gardner 1984). The grass can be eradicated by spraying with 0.5% glyphosate (Gardner and Kageler 1983) or Dalapon (Hosaka 1958).

It is found on all major islands from 500-2,000 m in dry and mesic habitats. It will also invade wet environments when the forest is disturbed. It has been classified as a noxious weed by the U.S. Department of Agriculture in all states except Hawai'i.

Pennisetum setaceum (Forsk.) Chiov. (Fountaingrass)
This bunchgrass is a noxious weed, crowding out other herbs and seedlings. It is a fire-stimulated grass which carries intense fires throughout its range. The seeds are dispersed by wind. Any attempt to evaluate its potential for biological control will be undoubtedly opposed by the sugar industry.

It is present on all major islands with the major infestation on the Kona side of Hawai'i.

Phormium tenax J.R. and G. Forst. (New Zealand flax)
This rosette-like lily forms dense thickets from which other species are excluded. Man is probably the principal dispersal agent but granivorous birds cannot be completely discounted. Adaptation to fire is unknown, and it has not been evaluated for biological control.

The species is found principally in gullies in mesic areas below 300 m, e.g. Moloka'i, and the northern Hamakua coastline, Hawai'i.

Pinus caribaea Morelet (Slash pine)
This evergreen tree can form dense monotypic stands reaching 15 m in height displacing all other plants. The seeds are dispersed by wind, and it is rapidly destroyed by fire. Control in native ecosystems is by felling. It has not been evaluated for biological control because it is still hoped that it will produce timber for a forest industry.

The principal infestation is on Moloka'i.

Pinus patula Schlecht. and Cham. (Mexican weeping pine)
The problems with this pine are very similar to P. caribaea. The principal infestation is in the area adjacent to Hosmer Grove, Haleakala National Park, Maui.

Pinus pinaster Ait. (Cluster pine)

The problems with this pine are very similar to those with P. caribaea. The principal infestation is in the Polipoli area, Maui between 1,600-2,200 m elevation.

Pithecelobium dulce (Roxb.) Benth. (Opiuma)

This thorny, deciduous tree grows up to 10 m tall, forming impenetrable thickets. The seeds are dispersed by alien frugivorous birds. It is relatively resistant to fire and resprouts rapidly by basal or aerial shoots. The tree has not been evaluated for biological control, a strategy that would probably be opposed because of its use in landscaping.

It is found from sea level to 300 m elevation in dry habitats. Major infestations are at Mokule'ia, O'ahu; the east end of Moloka'i; the gulches east of Lahaina, Maui; and South Kona, Hawai'i.

Pluchea indica (L.) Less. (Indian fleabane)

The problems associated with this species are similar to P. odorata. This plant is confined to lowland habitats, particularly wetlands and fishponds. There is a major infestation at Kanaha pond, Maui.

Pluchea odorata (L.) Cass. (Sour bush)

This 1-2 m tall, fast-growing shrub forms thickets in dry habitats. The seeds are wind-dispersed. Its resistance to fire depends on the intensity of the fire. It generally regenerates from basal shoots. Some biological control agents have been introduced but they have not been effective.

It is found on all major islands from sea level to 1,000 m elevation.

Prosopis pallida (Humb. and Bonpl. ex Willd.) HBK. (Kiawe, mesquite)

This deciduous, thorny tree grows up to 20 m tall. It overshadows other vegetation but also desiccates an area by using all available water. Deep root systems tap ground-water. There is no known disseminator of the seeds but mesquite was planted in arid areas for shade and reforestation. The pods were used extensively for fodder, resulting in further dissemination or intensification of stands. This species is generally killed by intense fires, although a small proportion of the trees will survive if the bases are partially protected. It has not been evaluated for biological control. It has many uses (Simpson 1977) and is locally favored by bee-keepers.

The plant is found in arid regions on all islands between sea level and 700 m. In dry areas dense populations are found over subterranean water courses.

Psidium cattleianum Sabine (Strawberry guava)

This medium-sized tree forms dense thickets, later forming forests under which very few other plants grow. It is the worst pest in Hawai'i's rain forests. It is favored by pigs which move into infested areas during the fruiting season in the fall. The seeds pass through digestive tracts unharmed and are often deposited in soil disturbed by pigs. Alien frugivorous birds also disperse the seed, often in areas without soil disturbance. In this case, infestations spread very slowly. Adaptation to fire is unknown. The prospects for biological control are slim because the commercial exploitation of the common guava would require rigorous species specificity of the control agent. However, the extent of the infestation of this species precludes any other approach.

Strawberry guava is found on all major islands between 150-1,300 m, principally in rain forest habitats.

Psidium guajava L. (Guava)

This evergreen tree reaches heights of 8 m. It invades disturbed sites and forms dense thickets. The leaves are suspected of allelopathic activity. The seeds are dispersed by alien frugivorous birds as well as rats and feral pigs. Guava can survive moderately intense fires by regenerating from basal sprouts. It has not been evaluated for biological control and is unlikely to be because of commercial orchards on Kaua'i and Hawai'i.

It is distributed in mesic to wet areas below 500 m on all major islands, and in gulches, even in dry areas.

Rhizophora mangle L. (Red mangrove)

This evergreen tree grows up to 25 m tall in coastal marshes and streams. The monotypic stands form a very dense cover, excluding all other species. On O'ahu and Moloka'i, these infestations have significantly altered almost all brackish water ecosystems as well as many fishponds. The seedlings are dispersed by water. Red mangrove forests are generally destroyed by fire, but the species has not been evaluated for biological control.

It is confined to brackish waters around all major islands.

Rhodomyrtus tomentosa (Ait.) Hassk. (Rose myrtle)

This noxious evergreen shrub rarely grows above 3 m but forms dense thickets. The seeds are dispersed by alien frugivorous birds. Its adaptation to fire is unknown, and it has not been evaluated for biological control.

The plant grows in lowland mesic habitats. There is a major infestation on Kaua'i, particularly in Kilohana Crater. It is displacing Melastoma malabathricum in some areas.

Ricinus communis L. (Castorbean)

This fast-growing tree can reach heights of 10 m. It forms somewhat ephemeral thickets which can shade out other species. Although rodents and granivorous birds may disperse some seeds, man is the principal agent. Castorbean is destroyed by fire; it has not been evaluated for biological control.

It grows in dry and mesic habitats from sea level to 1,200 m on all major islands.

Rubus argutus Link (R. penetrans Bailey in Hawaiian literature) (Florida prickly blackberry)

This thorny scrambler is a noxious weed which rapidly invades disturbed areas between 1,000-2,300 m. It forms impenetrable thickets which expand by the rooting of aerial shoots where they bend over and touch the ground. Alien frugivorous birds are the principal dispersal agents. The aerial portions of a plant are normally destroyed by fire but the plant quickly recovers from basal and subterranean shoots. Several biological control agents have been introduced but they are not very effective. Two rust diseases are currently under investigation by the National Park Service (NPS) and U.S. Forest Service (USFS). Some biocontrol agents introduced to control this species have adversely affected the 2 native Rubus species.

The species is well established in mesic to wet forests on all major islands.

Rubus ellipticus Sm. (Yellow Himalayan raspberry)

This prickly, semi-deciduous shrub invades native forests principally in pig-disturbed areas. The plants spread into neighboring forest from underground shoots. The seeds are dispersed by alien, and perhaps native, frugivorous birds. The species regenerates rapidly from underground shoots after fire. It has not been evaluated for biological control except collectively with other Rubus species (Gardner and Davis 1982).

It is found in wet habitats between 700-1,700 m, and there is a major infestation at Volcano, Hawai'i.

Rubus glaucus Bth. (Raspberry)

This species is similar in many respects to R. ellipticus. It was introduced at Volcano and Pa'auilo Agricultural Experimental Stations, where it grew but did not provide commercially exploitable fruit crops. The canes were abandoned but the seeds were dispersed by birds; the plant is now threatening the 'Ola'a Tract of Hawai'i Volcanoes National Park.

Rubus moluccanus L.

This species is a very serious pest similar to R. argutus. There is a major infestation at Koke'e, Kaua'i.

Rubus nivalis Doug. ex Hook.

This species is also a very serious pest similar to R. argutus. There are major infestations at Polipoli, Maui, and Humu'ula, Hawai'i.

Sacciolepis indica (L.) Chase (Glenwood grass)

This slender, annual grass invades disturbed and open areas in wet habitats. The seeds are dispersed by sticking to animal fur. Its response to fire, an unlikely event in the rain forest, is unknown. It has not been evaluated for biological control.

Glenwood grass occurs on all major islands. There is a large infestation moving into Wahiawa Bog, Kaua'i and above Nahiku, Maui.

Schinus terebinthifolius Raddi (Christmasberry)

The low-growing, evergreen, deciduous tree is an aggressive invader of most mesic to wet lowland environments. It shades out other plants, as well as prevents reestablishment of other species due to the release of allelopathic substances (Gogue, Hurst, and Bancroft 1974). The fruit is especially favored by alien frugivorous birds. Schinus is killed by high intensity fires but regenerates rapidly where there is a large seed bank. A defoliating insect has been introduced but has not been effective. Further attempts at biological control can be expected to be met with stiff opposition from bee-keepers.

The species is widely distributed in lowland areas of all major islands.

Senecio mikanioides Otto ex Walp. (German ivy)

This noxious, light-loving vine grows rapidly into the emergent layers of forests where it festoons the vegetation. The seeds are wind-dispersed. The degree of adaptation to fire is unknown, and it has not been evaluated for biological control.

Senecio grows in open, wet habitats between 800-2,000 m. There are several infestations along the Saddle Road, e.g., Pu'u Huluhulu, Hawai'i, and it is becoming established at upper elevations on Mauna Kea and Manuka. The infestations there are local and could still be controlled with mechanical methods.

Setaria palmaefolia (Koen.) Stapf (Palmgrass)

This large-leaved, perennial grass reaches heights of almost 2 m, shading out other herbaceous vegetation. The seeds are distributed passively or by granivorous birds. The young shoots are eaten by feral pigs, which intensify infestations by uprooting neighboring vegetation, creating new areas for establishment. Palmgrass is well-adapted to fire. It has not been evaluated for biological control.

It is found in wet areas on all major islands from 300-2,000 m elevation. There are major infestations in the 'Ola'a, Hilo, Kohala, and Wai'akea Forest Reserves, Hawai'i, and the Ko'olau Forest Reserve, Maui.

Spathodea campanulata Beauv. (African tuliptree)

This showy, shade-tolerant, evergreen tree reaches heights of 25 m. It invades abandoned agricultural land and closed forest where the wind-dispersed seeds germinate rapidly. These seedlings continue growing, forming thickets from which a few saplings may reach the canopy. Adaptation to fire is unknown, and it has not been evaluated for biological control.

Tuliptree occurs in wet habitats from sea level to 1,000 m on all major islands. There are major infestations tucked away in almost every rain forest valley along the northern and eastern slopes of Kaua'i, O'ahu, and East Maui.

Tagetes minuta L. (Marigold)

This noxious, rapidly growing herb forms a dense ground cover at higher elevations. The seeds cling to hair and are dispersed by domesticated and feral animals. It is killed by fire, but new colonies are formed rapidly from the seed bank. Marigold has not been evaluated for biological control.

The plant is confined to dry and mesic areas on Mauna Kea between 1,700-3,000 m.

Terminalia catappa L. (False kamani)

This evergreen tree rarely reaches heights over 15 m. It shades out all other species. The seeds are dispersed by man and probably by water. Adaptation to fire is unknown. It has not been evaluated for biological control and is considered a desirable shade tree by many people.

The plant is confined to mesic and wet coastal habitats on all major islands.

Tibouchina urvilleana (DC.) Cogn. (Glorybush)

This semi-deciduous shrub reaches heights of 4 m. It forms thickets in wet habitats. The seeds are mechanically dispersed from a capsule with sufficient force to enable this species to form expanding thickets in suitable habitats. Adaptation to fire is unknown. Gardner and Davis (1982) suggested that it had been partially controlled by Selca brunella Hampson, but no control has been effected at the principal infestations. Apart from that, the potential for biological control has not been exploited.

Tibouchina is confined to wet habitats between 200-1,700 m on Kaua'i, O'ahu, and Hawai'i. There is a major infestation in Volcano, Hawai'i.

Ulex europaeus L. (Gorse)

This noxious, spiny shrub reaches heights of 2 m. It forms impenetrable, monotypic thickets. The seeds are forcibly ejected up to 3 m from the parent plant. Long-distance dispersal is effected by man or by capsules attached to branches entangled in mammal pelage. Although much of the aerial portion of the plant may be destroyed by fire, the remaining portions regenerate rapidly. Fire also aids in breaking the dormancy of the seeds. Gorse has been subjected to biological control, the effectiveness of which has been reviewed by Markin (1984).

It grows in mesic habitats between 200-2,100 m on Maui and Hawai'i. The infestations at Olinda, Maui and Humu'ula, Hawai'i are a considerable problem and beyond economically feasible mechanical or chemical control.

Verbascum thapsus L. (Common mullein)

This wooly, biennial, rosette plant forms a dense ground cover displacing slower-growing native species. The seeds are wind-dispersed. Fires are retarded in stands of this plant under normal conditions. Mullein has been partially controlled by a gall-forming insect which has reduced population size and range significantly.

The plant is found between 2,200-3,100 m on Mauna Kea, Hawai'i.

Additional Species

The following species now found in Hawai'i need to be monitored because their behavior elsewhere suggests that they could become serious pests.

- Acacia melanoxylon R.Br. (Australian blackwood)
- Ailanthus altissima (Mill.) Swingle (Tree of Heaven)
- Anisomeris fasciculata K. Schum.
- Athyriopsis japonica (Thunb.) Ching
- Blechnum occidentale L. (Blechnum fern)
- Brugeria gymnorhiza (L.) Lam. (Oriental mangrove)
- Buddleja madagascariensis Lam. (Butterfly bush)
- Caesalpinia bonduc (L.) Roxb. (Yellow knickers)
- Castilloa elastica Cerv. (Panama rubber tree)
- Cecropia obtusifolia Bertol. (Guaramo)
- Cinchona succirubra Pav. ex Klotsch. (Quinine tree)
- Cordia glabra L. (Broad-leaved cordia)
- Eleagnus multiflora Thunb. (Gumi)
- Eucalyptus globosus Labill. (Blue gum)
- Euphorbia ?antiquorum L. (Cactus-like spurge)
- Flindersia brayleyana F. Muell. (Silkwood)
- Haematoxylon campechianum L. (Logwood)
- Heterocentron subtriplinervium (Link and Otto) A. Br. & Bouche (Pearl flower)
- Hunnemannia fumariaefolia Sweet (Mexican tulip poppy)
- Mimosa invisa Mart.
- Montanoa hibiscifolia (Benth.) C. Koch (Montanoa)
- Oxyspora paniculata (D. Don) DC.
- Passiflora edulis Sims (Liliko'i)
- Passiflora laurifolia L. (Yellow granadilla)
- Samanea saman (Jacq.) Merr. (Monkeypod)
- Swietenia mahogani (L.) Jacq. (Mahogany)
- Terminalia myriocarpa Heurck and Muell.-Arg. (Jhalna)
- Thunbergia alata Bojer ex Sims (Black-eyed Susan)
- Thunbergia grandiflora Roxb. (Large-flowered thunbergia)
- Thunbergia laurifolia Lindl. (Laurel-leaved thunbergia)
- Trema orientalis (L.) Bl. (Charcoal tree)
- Urena lobata L. (Aramina)
- Wedelia trilobata (L.) Hitchc. (Wedelia)
- Wisteria sinensis Sweet (Chinese wisteria)

PROBLEM WEEDS IN HAWAI'I BY ISLAND

The determination that any weed is a pest is somewhat subjective. However, there is usually a general consensus about the most important weeds on each island. Seven species (Florida prickly blackberry, Christmasberry, common guava, Guinea grass, koa haole, lantana, and molassesgrass) are serious pests on all islands (table 1). They all occur in dry to mesic lowland environments, but lantana and molassesgrass are also found at higher elevations and in wetter habitats. Another 5 (common ironwood, swamp oak, Java plum, kiawe, and strawberry guava), although present on all islands, are a problem only on 5 islands. With the exception of swamp oak, they are not a problem on Lana'i because it is too dry for their proper development. Another 7 species (bamboo, Chinese banyan, faya tree, Indian fleabane, roseapple, Glenwood grass, and sourbush) are a problem on 4 islands only, but they may be present on all islands. Again these are species which prefer wetter habitats and are therefore excluded from Lana'i and some other islands.

All 19 species just noted are serious threats to native ecosystems or their reestablishment. They all smother vegetation, displacing the native species or preventing their reestablishment. Egler (1942) has suggested that koa haole will enhance recolonization of native species by ameliorating the habitat. There is little evidence to support this hypothesis. In fact, it appears that the native species are being excluded from these environments and their seed banks exhausted.

Fourteen other species (African tuliptree, ardisia, banana poka, bush beardgrass, broomsedge, cats-claw, fountaingrass, Indian rhododendron, kahili ginger, kikuyugrass, Kosters curse, palmgrass, velvetgrass, and white ginger) are a serious problem on 2 or 3 islands but have not yet filled their potential range. With the exception of bush beardgrass, cats-claw, fountaingrass, and velvetgrass, they all infest wet habitats. Broomsedge and kikuyugrass infest dry, mesic, and wet habitats.

Seven species (buffelgrass, gorse, hairy cats-ear, kahili flower, _Rubus nealus_, sweet vernalgrass, and white ginger) are problems only on Maui and Hawai'i. Hairy cats-ear, _Rubus nealus_, and sweet vernalgrass are confined to high elevations. Gorse was introduced to the higher elevations of Haleakala and Mauna Kea only but would grow in mesic habitats above 200 m on all islands. Buffelgrass is a serious weed in very dry areas. It is not clear why white ginger infestations are confined to Maui and Hawai'i, as suitable habitat exists on other islands.

Table 1. Continued.

Scientific Name (Common Name)	Island						Nox-ious	Allel-opath	N_2 Fix.	Why Intro.	Where From	Fire Sus.	Growth Form
	Kau	Oah	Mol	Lan	Mau	Haw							
Bambusa sp. (Bamboo)	+	+	+		+	(+)				Hort	Asia	C	Ph
Bidens pilosa (Beggar's tick)	(+)	(+)	(+)	(+)	+	(+)				Inad	TrAm	A	Th
Bocconia frutescens					+	(+)				Hort	TrAm		Ch
Brachiara mutica (California grass)	(+)	+	(+)	(+)	(+)	(+)		Y		Fodd	Afrc	B	HC
Brassaia actinophylla (Octopus tree)	+	+	(+)		(+)	(+)				Hort	Aust	D	Ph
Caesalpinia sepiaria (Cats-claw)	+	+			+	(+)	Y		?	Hort	Asia		Li
Casuarina equisetifolia (Common ironwood)	+	+	+	(+)	+	+		Y	Y	Eros	Aust	C	Ph
C. glauca (Swamp oak)	(+)	+	+	+	+	+		Y	Y	Eros	Aust	C	Ph
Cecropia peltata (Trumpet tree)	(+)	+	(+)		(+)	+				Hort	TrAm	D	Ph
Cenchrus ciliaris (Buffelgrass)	(+)	(+)	(+)	(+)	+	+				Eros	Afrc	B	HC

Table 1. List of weed pests in Hawai`i, showing distribution by island; whether or not noxious, allelopathic, or able to fix N_2; why introduced and where from; susceptibility to fire; and growth form. [(+) = present but not a pest; + = pest].

Scientific Name (Common Name)	Island						Nox-ious	Allel-opath	N_2 Fix.	Why Intro.	Where From	Fire Sus.	Growth Form
	Kau	Oah	Mol	Lan	Mau	Haw							
Acacia mearnsii (black wattle)	(+)	(+)	(+)	(+)	+	(+)	Y[1]	(Y)	Y	Eros[2]	Aust[3]	A[4]	Ph[5]
A. confusa (Formosan koa)	(+)	+	(+)	(+)	+	(+)		Y	Y	Eros	SEAs	C	Ph
A. farnesiana (Klu)	+	+	(+)	(+)	(+)	(+)			Y	Inad	TrAm	A	Ph
Albizia falcataria (Molucca albizia)	+	+	(+)	(+)	(+)	+			Y	Fsty	SEAs		Ph
Andropogon glomeratus (Bush beardgrass)						+		Y		Inad	NoAm	B	Ch
A. virginicus (Broomsedge)	(+)	+	+	(+)	(+)	+		Y		Inad	NoAm	B	Ch
Anthoxanthum odoratum (Sweet vernalgrass)					+	+				Fodd	Eurp	A	HC
Ardisia humilis (Shoebutton ardisia)	(+)	+			+	(+)				Hort	Asia		Ph
Asystasia gangetica (Asystasia)										Hort	Asia	B	Ch

Table 1. List of weed pests in Hawai`i, showing distribution by island; whether or not noxious, allelopathic, or able to fix N_2; why introduced and where from; susceptibility to fire; and growth form. [(+) = present but not a pest; + = pest].

Scientific Name (Common Name)	Island						Nox-ious	Allel-opath	N_2 Fix.	Why Intro.	Where From	Fire Sus.	Growth Form
	Kau	Oah	Mol	Lan	Mau	Haw							
Acacia mearnsii (black wattle)	(+)	(+)	(+)	(+)	+	(+)	Y[1]	(Y)	Y	Eros[2]	Aust[3]	A[4]	Ph[5]
A. confusa (Formosan koa)	(+)	+	(+)	(+)	+	(+)		Y	Y	Eros	SEAs	C	Ph
A. farnesiana (Klu)	+	+	(+)	(+)	(+)	(+)			Y	Inad	TrAm	A	Ph
Albizia falcataria (Molucca albizia)	+	+	(+)	(+)	(+)	+			Y	Fsty	SEAs		Ph
Andropogon glomeratus (Bush beardgrass)						+		Y		Inad	NoAm	B	Ch
A. virginicus (Broomsedge)	(+)	+	+	(+)	(+)	+		Y		Inad	NoAm	B	Ch
Anthoxanthum odoratum (Sweet vernalgrass)					+	+				Fodd	Eurp	A	HC
Ardisia humilis (Shoebutton ardisia)	(+)	+			+	(+)				Hort	Asia		Ph
Asystasia gangetica (Asystasia)										Hort	Asia	B	Ch

Table 1. Continued.

Scientific Name (Common Name)	Island						Nox-ious	Allel-opath	N_2 Fix.	Why Intro.	Where From	Fire Sus.	Growth Form
	Kau	Oah	Mol	Lan	Mau	Haw							
Bambusa sp. (Bamboo)	+	+	+		+	(+)				Hort	Asia	C	Ph
Bidens pilosa (Beggar's tick)	(+)	(+)	(+)	(+)	+	(+)				Inad	TrAm	A	Th
Bocconia frutescens					+	(+)				Hort	TrAm		Ch
Brachiara mutica (California grass)	(+)	+	(+)	(+)	(+)	(+)		Y		Fodd	Afrc	B	HC
Brassaia actinophylla (Octopus tree)	+	+	(+)		(+)	(+)				Hort	Aust	D	Ph
Caesalpinia sepiaria (Cats-claw)	+	+			+	(+)	Y		?	Hort	Asia		Li
Casuarina equisetifolia (Common ironwood)	+	+	+	(+)	+	+		Y	Y	Eros	Aust	C	Ph
C. glauca (Swamp oak)	(+)	+	+	+	+	+		Y	Y	Eros	Aust	C	Ph
Cecropia peltata (Trumpet tree)	(+)	+	(+)		(+)	+				Hort	TrAm	D	Ph
Cenchrus ciliaris (Buffelgrass)	(+)	(+)	(+)	(+)	+	+				Eros	Afrc	B	HC

Scientific Name (Common Name)	Island						Nox-ious	Allel-opath	N_2 Fix.	Why Intro.	Where From	Fire Sus.	Growth Form
	Kau	Oah	Mol	Lan	Mau	Haw							
Citharexylum caudatum (Juniper berry)		+								Hort	TrAm		Ph
C. spinosum (Fiddlewood)	(+)	+			(+)	(+)				Hort	TrAm		Ph
Clerodendron fragans (Glorybower)	+		(+)			(+)				Hort	SEAs		Ch
Clidemia hirta (Koster's curse)	+	+	+		+	+	Y			Eros	TrAm		Ch
Corynocarpus laevigatus (New Zealand laurel)	+					(+)				Hort	NZ		Ph
Eugenia cumini (Java plum)	+	+	+	(+)	+	+		(Y)		Hort	SEAs	C	Ph
E. jambos (Roseapple)	+	+	(+)		+	+				Hort	TrAm	C	Ph
Ficus microcarpa (Chinese banyan)	+	+	(+)	(+)	+	+		(Y)		Hort	SEAs	C	Ph
Fraxinus uhdei (Mexican ash)	(+)	+	+	(+)	(+)	(+)				Fsty	TrAm		Ph
Furcraea foetida (Mauritius hemp)	+	+	(+)	(+)	(+)	(+)				Hort	SoAm	C	Ph

Table 1. Continued.

Scientific Name (Common Name)	Island						Nox-ious	Allel-opath	N_2 Fix.	Why Intro.	Where From	Fire Sus.	Growth Form
	Kau	Oah	Mol	Lan	Mau	Haw							
Grevillea banksii (Kahili flower)	(+)	(+)	(+)		+	+	Y	Y		Inad	Aust	A	Ph
G. robusta (Silky oak)	(+)	(+)	(+)	(+)	+	+		Y		Fsty	Aust	A	Ph
Hedychium coronarium (White ginger)	(+)	(+)	(+)		+	+				Hort	Asia		Ge
H. flavescens (Yellow ginger)	+	(+)	(+)		(+)	+				Hort	Asia		Ge
H. gardnerianum (Kahili ginger)	+	(+)	(+)		+	+				Hort	Asia		Ge
Heliocarpus popayensis (White moho)	(+)	+				+				Fsty	TrAm		Ph
Holcus lanatus (Velvetgrass)	(+)	(+)	(+)	(+)	+	+				Fodd	Eurp	A	HC
Hypochoeris radicata (Hairy cats-ear)					+	+				Inad	Eurp	A	Ge
Lantana camara (Lantana)	+	+	+	+	+	+	Y	Y		Hort	TrAm	A	Ch
Leptospermum ericoides (Tree manuba)				+				(Y)		Hort	NZ	A	Ph

Scientific Name (Common Name)	Island						Nox-ious	Allel-opath	N_2 Fix.	Why Intro.	Where From	Fire Sus.	Growth Form
	Kau	Oah	Mol	Lan	Mau	Haw							
L. scoparium (New Zealand tea)		+		+	(+)	(+)		Y		Hort	NZ	A	Ch
Leucaena leucocephala (Koa haole)	+	+	+	+	+	+			Y	Fodd	TrAm	B	Ph
Linociera intermedia (Olive)						+		(Y)		Hort	Asia		Ph
Melaleuca leucadendra (Paperbark)	(+)	+	(+)	(+)	+	+		Y		Fsty	Aust	A	Ph
Melastoma malabathricum (Indian rhododendron)	+	+				+	Y			Hort	Asia		Ph
Melia azedarach (Pride of India)	(+)	+	(+)	(+)	(+)	(+)				Hort	Asia		Ph
Melinis minutiflora (Molassesgrass)	+	+	+	+	+	+				Fodd	Afrc	B	HC
Melochia umbellata (Melochia)	(+)	(+)				+				Fsty	Asia		Ph
Merremia tuberosa (Woodrose)	+	(+)	(+)	(+)	(+)	(+)				Hort	SEAs	B	Li
Miconia magnifica						+				Hort	SEAs?		Ph

Table 1. Continued.

Scientific Name (Common Name)	Island Kau	Oah	Mol	Lan	Mau	Haw	Nox-ious	Allel-opath	N_2 Fix.	Why Intro.	Where From	Fire Sus.	Growth Form
Microlaena stipioides (Meadow ricegrass)	(+)	(+)	(+)	(+)	(+)	+				Inad	Aust	A	HC
Myrica faya (Fayatree, Firetree)	+	+		+	(+)	+	Y	Y		Eros?	Eurp	A	Ph
Panicum maximum (Guinea grass)	+	+	+	+	+	+		Y		Fodd	Afrc	B	Ch
Paspalum conjugatum (Hilo grass)	(+)	(+)	+		+	+		(Y)		Fodd	SoAm		HC
Passiflora ligularis (Sweet granadilla)	(+)					+				Hort	TrAm		Li
P. mollissima (Banana poka)	+				+	+				Hort	TrAm		Li
P. suberosa (Huehue-haole)	(+)	+			+					Hort	TrAm	D	Li
Pennisetum clandestinum (Kikuyugrass)	+	(+)	(+)	(+)	+	+		Y		Fodd	Afrc	C	HC
P. setaceum (Fountaingrass)		(+)			(+)	+	Y	(Y)		Hort	Afrc	B	HC
Phormium tenax (New Zealand flax)	(+)		(+)	(+)	(+)	+				Hort	NZ	C	Ph

Scientific Name (Common Name)	Island						Nox-ious	Allel-opath	N_2 Fix.	Why Intro.	Where From	Fire Sus.	Growth Form
	Kau	Oah	Mol	Lan	Mau	Haw							
<u>Pinus elliottii</u> (Slash pine)	(+)		+	(+)	(+)	(+)				Fsty	TrAm	D	Ph
<u>P. patula</u> (Mexican weeping pine)		(+)			+	(+)				Fsty	TrAm	D	Ph
<u>P. pinaster</u> (Cluster pine)			(+)	(+)	+	(+)				Fsty		D	Ph
<u>Pithecelobium dulce</u> (Opiuma)	(+)	+	+		(+)	+			Y	Hort	TrAm	A	Ph
<u>Pluchea indica</u> (Indian fleabane)	+	+	(+)	(+)	+	+				Inad	Asia	B	Ch
<u>P. odorata</u> (Sourbush)	+	+	(+)	(+)	+	+				Inad	TrAm	B	Ch
<u>Prosopis pallida</u> (Kiawe)	+	+	+	(+)	+	+			Y	Fodd	TrAm	D	Ph
<u>Psidium cattleianum</u> (Strawberry guava)	+	+	+	(+)	+	+		(Y)		Hort	TrAm		Ph
<u>P. guajava</u> (Common guava)	+	+	+	+	+	+		Y		Hort	TrAm		Ph
<u>Rhizophora mangle</u> (Red mangrove)	(+)	+	+	(+)	(+)	+		(Y)		Eros	TrAm	D	Ph

Table 1. Continued.

Scientific Name (Common Name)	Island						Nox-ious	Allel-opath	N_2 Fix.	Why Intro.	Where From	Fire Sus.	Growth Form
	Kau	Oah	Mol	Lan	Mau	Haw							
Rhodomyrtus tomentosa (Rose myrtle)	+	(+)					Y			Hort	SEAs		Ph
Ricinus communis (Castor bean)	+	(+)	(+)	(+)	(+)	+				Hort	Afrc	D	Ph
Rubus argutus (Florida prickly blackberry)	+	+	+	+	+	+	Y			Hort	NoAm	A	Ch
R. ellipticus (Yellow Himalayan raspberry)						+				Hort	Asia	A	Ch
R. glaucus (Raspberry)						+				Hort	TrAm	A	Ch
R. moluccana	+									Hort	SEAs	A	Ch
R. nivalis					+	+				Hort		A	Ch
Sacciolepis indica (Glenwood grass)	+	+	(+)		+	+				Fodd	SEAs		HC
Schinus terebinthifolius (Christmasberry)	+	+	+	+	+	+		Y		Hort	TrAm	A	Ph
Senecio mikanioides (German ivy)						+	Y			Hort	Afrc		Li

Scientific Name (Common Name)	Island						Nox-ious	Allel-opath	N_2 Fix.	Why Intro.	Where From	Fire Sus.	Growth Form
	Kau	Oah	Mol	Lan	Mau	Haw							
Setaria palmaefolia (Palmgrass)	(+)	(+)	(+)		+	+		(Y)		Hort	Asia	A	Ch
Spathodea campanulata (African tuliptree)	+	+	(+)	(+)	+	(+)				Hort	Afrc		Ph
Tagetes minuta (Marigold)						+	Y			Inad	SoAm	A	Th
Terminalia catappa (False kamani)	(+)	+	(+)	(+)	(+)	(+)				Hort	SEAs		Ph
Tibouchina urvilleana (Glorybush)	+	(+)			(+)	+				Hort	SoAm		Ph
Ulex europaeus (Gorse)					+	+	Y		Y	Hedg	Eurp	B	Ch
Verbascum thapsus (Common mullein)						+				Inad	Eurp		Ge

Table 1. Continued.

Scientific Name (Common Name)	Island Kau	Oah	Mol	Lan	Mau	Haw	Noxious	Allelopath	N_2 Fix.
Total	66	64	53	42	67	76	13	26	10
Total weeds present as pests	36	43	20	11	44	54			
Island area (sq km)	1,624	1,574	676	361	1,887	10,458			

[1] Y = Yes, (Y) = Suspected.

[2] Eros = erosion control or ground cover, Fodd = fodder plants, Fsty = forestry, Hedg = animal control, Hort = horticulture, Inad = inadvertent.

[3] Afri = Africa, Asia = India to China, Aust = Australia and Melanesia, Eurp = Europe, NoAm = North America, NZ = New Zealand, SEAs = South-east Asia, TrAm = Tropical America.

[4] A = Resprouts quickly; B = stimulated, cover increases; C = fire spread slowed; D = destroyed.

[5] Ch = Chamaephgytes; Ge = Geophytes; HC = Hemicryptophytes; Li = Lianes, Ph = Phanaerophytes; Th = Therophytes.

Twenty-eight species appear to be a problem on one island only. Fourteen (50%) of them occur on Hawai'i, 5 (18%) on Kaua'i, 4 (14%) on Maui, 3 (11%) on O'ahu, and 1 each (4%) on Lana'i and Moloka'i. Most of these species occur on other islands but have not escaped, probably because they have not been introduced into a suitable environment.

It is somewhat surprising that O'ahu does not have the highest number of problem weeds. It is the principal port of entry for the Islands as well as the location of 3 botanical gardens. It is the most probable area where weeds would become established. Gerrish and Mueller-Dombois (1980) found some support for this hypothesis in that an area close to the metropolitan area (Tantalus) did have more weeds present than a more remote area (Pupukea). Also, juniper berry and several other plants which now infest the southern Ko'olaus appear to have dispersed from the Lyon Arboretum. However, the largest number of weeds occur on the island of Hawai'i. Although no obvious single explanation is available, it is known that several ranchers on Hawai'i have introduced large numbers of plants and birds for various reasons, particularly at elevations between 800-1,700 m. The recent formation and volcanic activity of much of the Island and the large expanses of open forest may provide favorable conditions for alien plant establishment.

Like most Pacific islands, the northwestern Hawaiian Islands have been affected by man--either by guano mining or World War II. Nihoa and Necker have not been disturbed (Clapp, Kridler, and Fleet 1977). Some aliens are established on Pearl and Hermes Reef and French Frigate Shoals, but they are not doing well (Amerson, Clapp, and Wirts 1974; Amerson 1971). Laysan and Lisianski were devastated by rabbits. Some alien species, including Casuarina, were planted but they have not spread (Clapp and Wirtz 1975; Ely and Clapp 1973; Lamoureux 1963). Kure Atoll, on the other hand, has a predominantly alien flora (Woodward 1972).

PROBLEM WEEDS IN HAWAI'I BY VEGETATION ZONE

It is quite obvious that lowland ecosystems in Hawai'i have suffered the most disruption from alien species because of agriculture, fire, and urbanization. These disturbances have created ideal conditions for the establishment of weeds. The lowlands are also the principal points of entry of most introductions to the Islands. Therefore, unless weeds survive in the tropical lowlands, they rarely become established. Occasionally, plants originally cultivated as ornamentals at lower elevations reach higher elevations, where they escape, e.g., Senecio mikanioides. This generalization will not be tenable for much longer as larger communities become established in the cooler upper elevations at Koke'e, Kaua'i; Kula, Maui; and Volcano, Hawai'i. Typical ornamentals will be introduced and then escape, e.g. the recent escape of nasturtium, <u>Tropaeolum</u> <u>majus</u>, at Hawai'i Volcanoes National Park.

It is not possible to make any meaningful assessment of weed invasions of Hawaiian ecosystems on the basis of elevation because of the significant differences in climatic conditions around the major islands. Ripperton and Hosaka (1942) in an early description of Hawai'i's vegetation subdivided it into 10 zones. Krajina (1963) later refined this system into 14 zones, principally by further subdividing the high rainfall categories. These vegetation zones provide a convenient framework for a discussion of the impact of alien plants on Hawaii's vegetation (table 2). Because disturbance in each zone has varied quite considerably, the following remarks are generalizations illustrating trends.

Land below 300 m elevation receiving less than 500 mm of rain each year (Ripperton and Hosaka's Zone A) is now almost totally dominated by alien forbs and shrubs (table 2). Formerly open native scrub grasslands, these areas were the principal habitation of the aboriginal Hawaiians. The lands were greatly disturbed by fire and in many instances have been severely eroded. When fires were suppressed as western civilization took hold, the native vegetation began to recover. However, the introduction of koa haole and its subsequent aerial broadcasting resulted in its rapid colonization and ultimate domination of these areas. Other species which are common in this zone include Formosan koa, Indian fleabane, klu, Java plum, and sourbush. In areas with subsurface water, kiawe is dominant. Along the west coast of Hawai'i fountaingrass has become a serious pest and dominates many coastal and upland areas. Where cheap irrigation water is available and the soil is reasonably deep, sugar cane or other crops are grown. In the driest areas of most islands (e.g. Diamond Head and Ka'ena Point, O'ahu) a few native species still predominate.

Zone B, land below 1,000 m with an annual rainfall from 500-1,000 mm, has suffered a fate very similar to Zone A in areas where there is insufficient soil for agriculture. However, below 350 m and where irrigation water is available, sugar cane plantations, or more recently papaya and macadamia nut farms, have been developed. Above 200 m pineapple is cultivated where irrigation is not feasible. On land too steep for plantations, various timber trees were planted,

Table 2. List of weed pests in the Hawaiian Islands by vegetation zone (Krajina 1963). (+ = present as a pest, (+) = present but not a pest).

Scientific Name (Common Name)	Vegetation Zone									
	A	B	C1	C2	D1	D2	D3	E1	E2	E3
Acacia mearnsii (Black wattle)		(+)	+	+						
A. confusa (Formosan koa)	+	+	+							
A. farnesiana (Klu)	+	+	+							
Albizia falcataria (Molucca albizia)		(+)	+		+					
Andropogon glomeratus (Bush beardgrass)		+	+	+				+		
A. virginicus (Broomsedge)	+	+	+	+	(+)			+		
Anthoxanthum odoratum (Sweet vernal grass)							+	+	+	
Ardisia humilis (Shoebutton ardisia)			(+)		+					
Asystasia gangetica (Asystasia)	+	+								
Bambusa sp. (Bamboo)			+		+					
Bidens pilosa (Beggar's tick)	+	+	+	+	(+)					
Bocconia frutescens			+	+				+		
Brachiaria mutica (California grass)	(+)	(+)	+		+					
Brassaia actinophylla (Octopus tree)			+		+					

Table 2. Continued.

Scientific Name (Common Name)	Vegetation Zone									
	A	B	C1	C2	D1	D2	D3	E1	E2	E3
Caesalpinia sepiaria (Cats-claw)		+	+		(+)					
Casuarina equisetifolia (Common ironwood)	+	+	+		+					
C. glauca (Swamp oak)	+	+	+		+					
Cecropia peltata (Trumpet tree)			+		+					
Cenchrus ciliaris (Buffel grass)	+	(+)								
Citharexylum caudatum (Juniper berry)		+	+		+					
C. spinosum (Fiddlewood)		+	+	(+)	+					
Clerodendron fragrans (Glorybower)					+					
Clidemia hirta (Koster's curse)			+	(+)	+					
Corynocarpus laevigatus (New Zealand laurel)			+	+						
Eugenia cuminii (Java plum)	(+)	+	+		+					
E. jambos (Roseapple)			(+)		+	+				
Ficus microcarpa (Chinese banyan)		+	+		+					
Fraxinus uhdei (Mexican ash)		(+)	+	+	+	+				
Furcraea foetida (Mauritius hemp)	+	+								

Scientific Name (Common Name)	Vegetation Zone									
	A	B	C1	C2	D1	D2	D3	E1	E2	E3
Grevillea banksii (Kahili flower)		+	(+)	+						
G. robusta (Silky oak)		+	(+)	+						
Hedychium coronarium (White ginger)			+	+	+	+	(+)			
H. flavescens (Yellow ginger)			+	+	+	+	(+)			
H. gardnerianum (Kahili ginger)			+	+	+	+	(+)			
Heliocarpus popayensis (White moho)			+		+					
Holcus lanatus (Velvet grass)						+	+	+	+	
Hypochoeris radicata (Hairy cats-ear)							+	+	+	
Lantana camara (Lantana)	(+)	+	+	(+)	(+)					
Leptospermum ericoides (Tree manuba)			+		+					
L. scoparium (New Zealand tea)					+	+				
Leucaena leucocephala (Koa haole)	+	+	+							
Linoceria intermedia (Olive)		+	+	+						
Melaleuca leucadendra (Paper bark)			(+)	(+)	+	+				
Melastoma melabathricum (Indian rhododendron)			+	+	+					

Table 2. Continued.

Scientific Name (Common Name)	Vegetation Zone									
	A	B	C1	C2	D1	D2	D3	E1	E2	E3
Melia azedarach (Pride of India)	+	+								
Melinis minutiflora (Molassesgrass)		(+)	+	+	+	+				
Melochia umbellata (Melochia)			+		+					
Merremia tuberosa (Woodrose)		(+)	+		+					
Miconia magnifica					+					
Microlaena stipioides (Meadow ricegrass)							+	+	(+)	
Myrica faya (Fayatree, firetree)			(+)	+		+	+			
Panicum maximum (Guinea grass)		+	+		(+)					
Paspalum conjugatum (Hilo grass)				+	+	+	(+)			
Passiflora ligularis (Sweet granadilla)						+				
P. mollissima (Banana poka)						+	+			
P. suberosa (Huehue-haole)	+	+	+							
Pennisetum clandestinum (Kikuyugrass)		(+)	(+)	+				+	(+)	
P. setaceum (Fountaingrass)	+	+		(+)						
Phormium tenax (New Zealand flax)					+					

Scientific Name (Common Name)	Vegetation Zone									
	A	B	C1	C2	D1	D2	D3	E1	E2	E3
Pinus elliottii (Slash pine)					(+)	+				
P. patula (Mexican weeping pine)							+			
P. pinaster (Cluster pine)								+	(+)	
Pithecelobium dulce (Opiuma)	+	+								
Pluchea indica (Indian fleabane)	(+)	(+)	+		+					
P. odorata (Sourbush)	+	+	+		(+)					
Prosopis pallida (Kiawe)	+	+	(+)							
Psidium cattleianum (Strawberry guava)			+		+	+				
P. guajava (Common guava)		(+)	+		+					
Rhizophora mangle (Red mangrove)	(+)	(+)	(+)		(+)					
Rhodomyrtus tomentosa (Rose myrtle)			+		+					
Ricinus communis (Castor bean)	(+)	+	+							
Rubus argutus (Florida prickly blackberry)				+		+	+	(+)	(+)	
R. ellipticus (Yellow Himalayan raspberry)					+	+	+			
R. glaucus (Raspberry)					+					

Table 2. Continued.

Scientific Name (Common Name)	Vegetation Zone									
	A	B	C1	C2	D1	D2	D3	E1	E2	E3
_R._ _moluccana_				+		+	(+)			
_R._ _nivalis_						+				
Sacciolepis _indica_ (Glenwood grass)				+	+	+	(+)			
Schinus _terebinthifolius_ (Christmasberry)	+	+	+		+					
Senecio _mikanioides_ (German ivy)						+	+	+		
Setaria _palmaefolia_ (Palmgrass)					+	+				
Spathodea _campanulata_ (African tuliptree)					+	+				
Tagetes _minuta_ (Marigold)								+	+	
Terminalia _catappa_ (False kamani)			+		+					
Tibouchina _urvilleana_ (Glorybush)			+		+	+				
Ulex _europaeus_ (Gorse)				+		+	+		+	
Verbascum _thapsus_ (Common mullein)									+	

Total Weeds Present	23	38	54	27	50	25	17	12	10	0

principally for watershed management. Where cropping has been abandoned, the area is dominated by broomsedge, cats-claw, Christmasberry, Formosan koa, fountaingrass, guava, Indian fleabane, Java plum, klu, koa haole, Koster's curse, lantana, and sourbush.

There are some notable exceptions to this general description of Zone B. Along the coastline in areas subjected to salt-water spray, there is a specialized ecosystem dominated by Fimbristylis. This community is still predominantly native because most weeds cannot tolerate the salt-water stress. Where cattle graze, the small shrubs have disappeared due to trampling and overgrazing. Many of these stress-resistant native species also occur elsewhere. Above 300 m on old unweathered lava flows or where there are many boulders, pockets of native dry forest have survived, e.g. Auwahi, Maui. Unfortunately, these woodlands frequently have a heavy ground cover of alien grasses, e.g. kikuyugrass, as well as heavy infestations of lantana. Survival of such woodlands is tenuous because kikuyugrass inhibits seed germination (Sanchez and Davis 1969) and cattle graze anything that grows.

In areas between sea level and 1,300 m where the annual rainfall ranges from 1,000-1,500 mm (Zone C) and where there is sufficient soil, sugar cane, pineapple, and more recently macadamia nut, plantations are found below approximately 650 m. Above this elevation most of the native forests have been converted to grassland. Some forest plantations have also been established in this zone. Below 1,300 m large areas have been infested and are now dominated by common guava from sea level to 400 m and strawberry guava from 300-1,300 m. Below 400 m the worst weeds are bamboo, broomsedge, Christmasberry, fiddlewood, glorybush, common guava, Indian rhododendron, Java plum, kahili ginger, koa haole, Koster's curse, roseapple, rosemyrtle, sourbush, white ginger, and yellow ginger. Above 400 m, Christmasberry, fiddlewood, Java plum, roseapple and sourbush drop out and fayatree moves in. Although much of the land in Zone C would be suitable for cattle grazing, it is overwhelmed by guava unless pastures are heavily grazed or the guava poisoned. Very few species can survive the competitive exclusion, principally by shading, although allelopathy is also suspected. Pockets of native vegetation still survive, but if feral pigs are not excluded from these areas they will soon be converted into guava woodlands (Diong 1983).

In areas between sea level and 2,300 m where the annual rainfall exceeds 1,500 mm (Zone D), the land below 1,350 m has been greatly altered by agriculture. Sugar cane is grown below 500 m although some plantations reach above 650 m. The gullies at these lower elevations are forested by a tropical weed flora (i.e., African tulip tree, ardisia, bush beardgrass, broomsedge, gingers, glorybush, Hilo grass, Indian rhododendron, Koster's curse, palmgrass, and roseapple) in which few native species survive. Between approximately 650 and 2,500 m, much of the land has been designated forest reserve for watershed protection. These forested areas are also maintained as hunting preserves, particularly for feral pigs. Areas not in reserve status have been converted to montane parklands by cattle ranching. Below 1,200 m strawberry guava is frequently dominant, forming monotypic stands. Between 1,000 and 1,650 m alien species are creating significant problems, e.g. banana poka, broomsedge, gingers, gorse, and velvetgrass. However, there are large tracts of 'ohi'a forest, generally in wetter areas, that have not been invaded by alien species other than a few relatively unimportant herbaceous plants.

Between 1,650 and 2,200 m there are numerous mires which have been undisturbed until quite recently. On Kaua'i, few weeds have moved into the disturbed sites although _Juncus planifolius_ R. Br. has invaded the summit area of Wai'ale'ale (J. Canfield and R.L. Stemmermann, pers. comm.). On Haleakala, where feral pigs have destroyed the _Oreobolus furcatus_ tussock community in some mires, hairy cats-ear and velvetgrass have become established, although they are partially displaced by the _Oreobolus_ once disturbance ceases. The resistance of Hawaiian mires to alien plant invasion is unclear, but the environmentally suboptimal conditions of these areas for plant growth (Crawford 1983) may reduce the competitive advantage of the weeds.

In the inversion layer zone between 2,000 and 2,300 m, where the annual rainfall is less than 1,250 mm, the native koa forests have been converted to cattle ranches and few intact segments remain. Most of the grasses in these parklands are aliens, principally kikuyugrass, although a few native grasses remain. However, along with the introduction of favored pasture grasses, e.g. sweet vernal grass, a number of less desirable grasses (e.g., orchard grass and velvetgrass) became established and spread to other areas. The dense growth and allelopathic secretions of grasses prevent the successful germination of koa and other native seeds. In some instances, koa sucker growth is inhibited. However, even when suckers grow they are soon eaten back by cattle and goats.

Above 2,300 m (Zone E), depending on the elevation that the inversion level reaches, the annual rainfall is less than 1,250 mm. This is one of the least impacted areas and alien species are not common except on deep ash or where the forest has been opened by feral goats and sheep. Giant mullein, hairy cats-ear, sheep sorrel (Rumex acetosella L.), orchardgrass, and velvetgrass are the most common weeds in this environment. Above 2,650 m the climatic conditions are so severe that there is little vegetation (Hedberg 1951). Any plant that does emerge is promptly eaten by feral herbivores. These high elevation environments are generally protected from alien plant introductions because most of the ports of entry are in the tropical lowlands. Temperate species would have difficulty getting established at lower elevations. However, recently, 2 temperate weeds were introduced at Haleakala National Park (but fortunately immediately eradicated), indicating the danger of temperate weed introductions to Hawai'i's high elevation ecosystems during construction of roads and facilities. It is hoped that similar monitoring and precautions will be taken during the construction of the new telescopes and support facilities atop Mauna Kea.

IMPACT OF WEEDS ON HAWAIIAN ECOSYSTEMS

Weeds can have a number of very different effects on associated plants. Physical displacement of other species, either directly or indirectly, is the most frequent mode of action. They can also deprive associated plants of water or nutrients, particularly nitrogen, not so much the result of greater efficiency of uptake (Mahmoud and Grime 1976) but by absorbing their "fair share" of a generally limited resource. Allelopathy from root secretions (Martin and Rademacher 1960) or aerial portions (Sanchez and Davis 1969; Gogue, Hurst, and Bancroft 1974) is often a direct competitive action. Weeds also act as primary or alternate hosts for pests and diseases. All these impacts can undoubtedly be found in the activity of alien species on native ecological processes in Hawai'i. However, the most common impact is displacement when weeds colonize disturbed sites (e.g. pig diggings, burnt areas) and occupy them before the slower growing native species can reestablish. Other adverse effects not commonly associated with weed activity are discussed below.

Formation of Monotypic Stands

The replacement of a relatively diverse native ecosystem by monotypic stands of alien species is a serious disruption of the ecosystem. In Hawai'i, the loss of diversity in even small areas can have a devastating effect on the survival of species, many of which are already endangered, almost extinct, or confined to very small areas. For example, Cyanea superba, a candidate endangered species, is now restricted to 2 areas of less than 0.1 ha each in the Mokule'ia Forest Reserve on O'ahu. Most of its former habitats are now occupied by strawberry guava. Where it survives it is threatened by the overgrowth of weeds, fire, and feral animals. The highly restricted distributions of many endemic species are not understood but are probably related to loss of dispersability characteristic of many island species (Carlquist 1965). Native primary consumers rarely adapt to aliens, and in the majority of instances they are excluded from the alien ecosystems.

Strawberry guava was introduced in 1825 (St. John 1973) and soon established in the wild (Judd 1936). On most islands, nearly monotypic stands of this species infest hundreds of hectares of mesic and well-drained rain forest areas between 200 and 1,300 m. Vast areas of mature 'ohi'a and koa forests have a dense understory of strawberry guava. Native species regenerate rarely; some straggly specimens of native plants, e.g. Alyxia olivaeformis, Osmanthus sandwicensis, Psychotria mariniana, are able to survive under the guava. However, the prognosis for native ecosystem reestablishment in guava thickets is poor for 3 reasons. First, the shade is so deep that no seeds germinate, or if they do they die for lack of sufficient light. In old strawberry guava stands in mesic areas, there is no ground cover. In rain forest areas, Oplismenis hirtellus and Christella dentata dominate the ground cover. Second, the fruit is relished by feral pigs, which move into these thickets during the fruiting season (Diong 1983) and thoroughly disturb the ground. Seeds, unharmed by passage through the gut, are dispersed in pig feces, generally to another disturbed site where they have a competitive edge. Third, there is growing evidence of allelopathic activity in the fallen leaves.

The creation of monotypic stands of alien species may in fact be followed by a more disastrous event. As the weed exploits and exhausts the particular resource that it is able to use, it may outgrow itself. Or, as the natural processes of aging and diseases take their toll, the population may crash, resulting in accelerated erosion or further weed invasions, but rarely in the reestablishment of even a semblance of the original native ecosystem. These population crashes are not uncommon events elsewhere (Salisbury 1964) but as yet have not been recorded in Hawai'i. Such crashes rarely provide sufficient time for the orderly reestablishment of a diversified ecosystem.

Changing Fire Characteristics

Although Vogl (1969) proposed that fire is a frequent natural formative agent in Hawaiian ecology, Mueller-Dombois (1981) found in one area of Hawai'i Volcanoes National Park that carbon-dated charcoal deposits and other evidence suggested a very low frequency. Human activity and the introduction of weeds, particularly grasses, has changed that. Since 1910 most fires in the Park have been started by man (Smith, Parman, and Wampler 1980). Much of the area in the Park supports a scattered scrub forest separated by patches of very sparsely vegetated lava. Fires, ignited by infrequent lava flows, were not uncommon. However, these fires were small in area because of the natural firebreaks in the vegetation mosaic.

In the early 1970's the situation changed. The National Park Service began a major resource management program to rid the park of feral goats (Baker and Reeser 1972). A few years before, both bush beardgrass and broomsedge had invaded the area. After most goats were removed, the grasses were no longer grazed and consequently colonized the many ash-filled cracks in lava flows, creating a continuous ground cover between islands of native scrub forest. The flowering stalks of these species are persistent after death, creating excellent fuel. These grasses are fire-stimulated, rapidly resprouting from basal sprouts after burning.

The total area burned by fires in lowland ecosystems is now 2 orders of magnitude larger than before the invasion of these grasses, even though an aggressive program of fire suppression by Park staff has significantly diminished the sizes of individual fires. Rapid regeneration of grass overshadows the reestablishment of most native species whose cover and abundance are drastically reduced for many years after the fire. As if to add insult to injury, the grasses also secrete a very persistent allelopathic agent (Rice 1972). The native Styphelia tameiameiae (Cham.) F. Muell., a common shrub in this ecosystem, is not fire-tolerant and will be excluded from burnt areas until it is reintroduced.

Changing Soil-Water Regimes

Many weeds introduced into oceanic islands come from temperate areas of Europe and America. Their phenology is occasionally not in synchrony with local climatic conditions, which results in significant changes in the edaphic ecology of the area.

Broomsedge is a bunchgrass that became established in the Hawaiian Islands about 50 years ago. It quickly invaded open sites with a deep soil or ash deposit where the annual rainfall was above 100 mm. Originally from the southeastern United States, it has retained the phenological pattern of its native area (Sorensen 1980). However, as Mueller-Dombois (1973) pointed out, the dormant period for broomsedge coincides with the wettest months in the islands, so that water is retained in the soil instead of being depleted through evapotranspiration. Surface runoff results in increased rates of erosion, with slumping on steeper slopes. Under native evergreen rain forest canopies, water is transpired away rapidly and the remainder percolates through the soil. Erosion and slumping are rare.

Changing Nutrient Status

Volcanically active areas do not have mature soils. Instead they have either lava or ash substrata characterized by low levels of nitrates. Plants which grow in such areas are adapted to survive under these conditions. However, species that can fix nitrogen will have faster growth rates than natives. Eleven of the 86 alien plants listed in table 1 fix nitrogen. Nitrogen-fixers will also enrich the soil as their litter decomposes. The outcome is an enriched soil in which other plants may grow, potentially replacing the original occupants of the area.

Fayatree is capable of fixing nitrogen in root nodules containing the actinomycete *Frankia* (Mian, Bond, and Rodrigues-Barrueco 1976; Miguel and Rodriguez-Barrueco 1974). The invasion of *Myrica* is relatively recent so that no floristic changes have been noted to date. Bradshaw et al. (1964), Rorison (1968), Mahmoud and Grime (1976), Higgs and James (1969), and Whelan and Edward (1975) have all shown that species native to poor soils are no more efficient at absorbing mineral nutrients than those native to good soils. Mahmoud and Grime (1976) further demonstrated the exclusion of plants native to poor soils, when grown on good soil with the plants adapted to good soils. The converse was not true. In the case of *Myrica faya* there is the distinct possibility that by enriching the soil it will enhance its own survival, perhaps to the exclusion of the native species. A monotypic infestation is already present in Hamakua, Hawai'i, which perhaps exemplifies this phenomenon; however, the history is insufficiently known.

Mutually Beneficial Interaction between Alien Plants and Animals

The absence of terrestrial mammals in the Hawaiian fauna has resulted in the lack of defense mechanisms against such animals. The introduction of mammals, especially ungulates, produced a new selective pressure on the native flora. Coupled with simultaneous introduction of alien plants, many of which are components of early secondary succession in their native habitat, Hawaiian ecosystems were faced with serious threats to their integrity.

Animals which dig up subterranean foods as part of their normal foraging activity are frequently important disseminators of plant propagules and play a role in nutrient cycling. In their native habitats, such disturbance is followed by a successional series of vegetation ultimately leading to some sort of climax community. In Hawai'i a natural successional series of this nature does not exist. Disturbance here has a significant deleterious impact on the native ecosystem, destroying ground cover, damaging roots, and opening up the understory. Most native species cannot tolerate this disturbance; however, many aliens are dependent on it for their establishment. When the alien species is an important food resource for a feral animal, a mutually beneficial interaction will develop between the 2 species. The relationship between feral pigs and such plants as strawberry guava, banana poka, and hairy cats-ear illustrate this point. Pigs are attracted to the abundant fruit of strawberry guava and banana poka. As pigs forage for other foods they disturb the ground, providing a seedbed for the guava and poka. Seeds are defecated up to 48 hours after consumption. They germinate and grow rapidly, occupying the site before the native plants establish. In the case of cats-ear, pigs destroy the weeds by digging up and consuming the roots. However, the digging provides an ideal seedbed for the establishment of the numerous, wind-dispersed seeds of this species. Why native species do not germinate or grow as rapidly as aliens is not yet known but can be related to their role in succession and the type of seedbed to which they are adapted. In both examples, original infestations are intensified or expanded, providing even more food resources for pigs.

IMPACTS OF WEEDS ON OTHER TROPICAL AND SUBTROPICAL ISLANDS

With a few exceptions--i.e., African Banks, Amirante (Feare 1979); Caroline Atoll (Clapp and Silbey 1971); Gough Island (Wace 1966); Henderson Island (Melville 1979); Raine Island (Stoddart, Gibbs, and Hopley 1981); and Wilingili Atoll, Maldives (Spicer and Newbery 1979)--alien species have become weeds and serious pests on every island that man has visited. Island ecosystems have been invaded to a considerable extent, but generally only after disturbance by direct human influence, e.g., fire, plantations, and introduced herbivores. For brevity's sake, I will review the literature on tropical and subtropical areas only. There is an extensive literature on temperate and subantarctic islands which is beyond the scope of this paper.

Atlantic Ocean and Caribbean Sea

The effects of alien organisms have been studied on only a few islands, but enough information is provided in floristic accounts and notes on many other islands to allow a reasonable analysis of the status of weeds on most islands. Although the prehistoric flora of St. Helena is poorly known, one-third of the known endemic flora is extinct and no vestiges of former ecosystems remain. New Zealand flax is the most serious pest. Ascension Island was relatively barren on its discovery and apparently a dismal place (Duffey 1964; Melville 1979). Over a thousand species have been introduced to vegetate the island. Many of them are familiar weeds on tropical islands, but only Melinis minutiflora (locally known as greasy grass) forms extensive ground cover above 500 m. Barbados has been severely disturbed by sugar cane cropping, but there is a sizeable remnant of the seasonal forest (Watts 1970). Mahogany has invaded most communities and abandoned fields. Anisomeris fasciculata K. Schum., Cordia glabra L., and Haematoxylon campechianum L. are also common. In the outer Leeward Islands of the West Indies, alien species have invaded all ecosystems (Harris 1962, 1965; Loveless 1960). Haematoxylon campechianum and koa haole are perhaps the most prevalent weeds along with kiawe and several thorny Acacia spp., common guava, Guineagrass, and Bermudagrass (Cynodon dactylon (L.) Pers.). Although "the position of aliens ... is formidable," Harris concluded that once human interference stops, the native species will replace the currently dominant aliens. The Cayman Islands have been significantly disturbed by agriculture, and 2 species, false kamani and Colubrina asiatica (L.) Brongn., are both invading inshore areas of the islands (Sauer 1982). In the Tortuga Keys, common ironwood has formed a dense woodland on Loggerhead Key, but the remaining 10 keys have not been affected by the alien species (Stoddart and Fosberg 1981b). Except for the 2 mid-Atlantic islands, most other islands appear to be able to revert to near-native plant formations once human interference ceases.

Indian Ocean

The native vegetation of the following islands has been almost totally destroyed by human activity: Diego Garcia (Stoddart 1971), the coral islands north of Madagascar, except Aldabra (Stoddart 1967), and Rodriguez Island (Melville 1979). In addition, however, the situation on Madagascar is among the worst examples of human mediated destruction of native ecosystems in the world (Humbert 1927). Rauh (1979) stated that "in less than 200 years the green island of Madagascar has been transformed into a red sand island simply by the activity of Man!" Aldabra (Stoddart and Wright 1967), Reunion (Melville 1979), and the Seychelles (Stoddart and Fosberg 1981a) have been occupied or exploited for sugar cane or copra for some time, but substantial segments of native ecosystems are still present. Mauritius has been severely disturbed by sugar plantations, but a number of reserves were set up in 1944. However, their continued existence is threatened by Ligustrum walkeri Decne, strawberry guava, Rubus spp. and Ardisia spp.

Pacific Ocean

Most of the central Pacific atolls have been severely disturbed by man (Egler 1942; Fosberg 1953; Lee 1974). The atolls are such specialized habitats that alien species, although maintaining themselves, do not become disruptive elements of the ecosystem. On the high islands the picture is very different. Their diversity of habitats and isolation have resulted in the evolution of new species and unique associations of species. Unfortunately, due to "haphazard exploitation and development" the "sorry state of the Hawaiian islands, many of the Galapagos, [and] Juan Fernandez ... will be repeated" (Wace 1966). The recent forest cropping in Fiji is yet another example of destructive expoitation (Melville 1979). The disturbance creates avenues for the invasion of alien species which, once established, can dominate that area and invade other habitats. The weed pests in Hawai'i have been discussed already. Clidemia hirta is a serious weed in Fijian forests (Wester and Wood 1977) although it is under partial biocontrol (Simmonds 1933). Klu, lantana, Mimosa invisa, common guava, and Urena lobata have all been declared noxious (Mune and Parham 1967). In the Galapagos, Cinchona succirubra Pav. ex Klotz., common guava, and Digitaria decumbens Stent are all serious pests (van der Werff 1979). Miconia magnifica is invading the forests of Tahiti, overwhelming the native ecosystems (Whistler, in press). In Samoa, Castilloa elastica, Koster's curse, Funtumia elastica, Mikania micrantha and Passiflora laurifolia are serious forest weeds (Whistler, in press). Lantana, koa haole, and common guava are also present but do not form extensive dense stands. Yet, in Tonga they are the 3 worst weeds in the forests (G. Buelow, pers. comm.). In the Northern Marianas, koa haole is almost ubiquitous because of aerial seeding after World War II (C.S. Hodges, pers. comm.).

WHAT NEEDS TO BE DONE

Three separate programs are needed to manage the alien pest problem in Hawai'i:

1. Prevent further introductions.
2. Stop the disturbance of ecosystems.
3. Develop strategies to allow native species to reestablish themselves.

Prevent Further Introductions

The prevention of further importations of alien species is imperative if we are to manage our native habitats effectively. The money spent on controlling pests would be much better spent on productive enterprises. Resources will still be needed to educate people not to import biological material indiscriminately, as well as to intercept deliberate attempts to smuggle material into the State. An immediate political step would be to require that all future government-sponsored landscaping use native species or plants that are known not to naturalize in Hawai'i.

A total prohibition on importations is not necessary. However, an outright ban on certain plant groups is imperative, e.g. all melastomes. Fifteen species in this group have already been introduced, 3 of which are serious weeds (Plucknett and Stone 1961). Further importation of Rubus, grasses, passion fruit, and members of the Myrtaceae should be banned also, as should species known to be problems in other tropical islands. These include the following species (from lists cited in this paper): Anisomeris fasciculata, Funtumia elastica, Ligustrum walkeri, Mikania micrantha, Operculina ventricosa, and Passiflora rubra. Species known to be part of primary or secondary succession in tropical or subtropical areas should be evaluated before they are permitted entry. The evaluations should be conducted by a group of botanists familiar with weeds in tropical and temperate areas. They should be constituted as a State Commission similar to the Animal Advisory Commission. They should have the authority to ban outright any importation. Their recommendations should be addressed to the Boards of Agriculture and Land and Natural Resources, who would have the right to veto any recommendation permitting entry but not overrule a negative decision of the Commission. Applications for permission to import should follow a format similar to an environmental impact statement.

Without the cooperation of the general public, there is little likelihood that any preventive program will work. Public education is a Federal and State responsibility. The best place to conduct the education of tourists and visitors is on the plane prior to arrival in the Islands. A 5-minute "commercial" explaining the problem and the importance of preventing plant and animal introductions would be much more effective than the printed form currently handed out in an almost cavalier fashion by the airlines. "Honesty" boxes should be provided in the baggage claim area where people can discard material prior to leaving the airport. Confiscation of material should be minimized except from people who are bringing potentially hazardous material to the Islands. Quarantine of imported material is important to minimize the introduction of associated pests and diseases. A more visible and concerned presence by the State's agriculture inspectors at ports of disembarkation is also necessary. Periodic inspection of baggage similar to the procedure on departure for mainlands would help keep people honest. The constant disclaimer by the State that it does not have sufficient funds to support such a program is a tacit acknowledgement that it does not consider alien plant introductions to be a major problem. Failure to enforce current regulations has resulted in the importation of *Miconia magnifica* and its consequent establishment in Hilo, which may turn out to be a very serious problem.

Two recent brochures, "Beware of the Noxious Weed" and "Are You a Carrier?", published by Foster Botanic Garden, Honolulu, are a valuable first step toward educating the general public on weed problems in Hawai'i. Much more needs to be done.

Stop Disturbance of Ecosystems

Many biologists have stressed the relationship between disturbance of ecosystems and alien establishment (e.g., Harper 1965; Stone, this volume). Two separate actions are necessary to reduce disturbance. The first is to change the State Constitution so that preservation of the State's natural resources is really mandated of the land managers. The second is to develop feral ungulate management programs to the point that the native forests are no longer significantly disturbed by these animals.

The State's Constitution is somewhat ambiguous regarding its natural resources. On the one hand, it talks about preservation and on the other, about the benefit of the public. The latter is currently interpreted as permitting exploitation. Some steps have been taken in the right direction. The State's Natural Area Reserve System, although originally an enlightened program, has become emasculated by politics and lack of finances and manpower. The number of areas formally designated is low. But even after areas are designated, no management is conducted because there are no funds allocated for that purpose. The resources of these areas are poorly known and research is discouraged by a cumbersome, time-consuming bureaucracy. Yet disturbances continue, sometimes on a large scale, resulting in the further degradation of ecosystems and the continued spread of alien species. Cooperation among the various government agencies with responsibilities in this area could also result in more effective management of pests. The recent signing of a memorandum of agreement between various State and Federal agencies regarding forest pest control is encouraging. However, the contributions of each of the agencies will be largely influenced by the internal budgets of each.

We have to accept the fact that feral ungulates are here to stay. However, it is possible to keep them out of areas not now infested, e.g. Oloku'i, Moloka'i; much of the Alaka'i Swamp, Kaua'i; Pu'u Kukui, 'Eke Crater, and Lihau Peak, West Maui; and to exclude them from important areas, e.g. national parks, State Natural Area Reserves, and the critical habitats of endangered and threatened species. The practice of maintaining sustained yields of animals by regulating the number of animals taken in forest reserves and other conservation areas should cease. This approach aggravates the alien plant problem by ensuring some level of perpetual disturbance in the forests.

Develop Strategies to Encourage Native Species Reestablishment

Two programs are needed. The first is the formulation and implementation of research on the biology of the most troublesome weeds. The second is the development of an integrated pest management system.

The most basic research questions concern location and effects of alien species. If sufficient historical information on infestations is available, and there generally is a wealth of anecdotal information, the dynamics of the invasion can be described. The most susceptible habitats can be identified and measures adopted to contain or prevent outbreaks in areas where management is possible. By evaluating the biology of the alien, it is sometimes possible to identify critical points in the life cycle when it is susceptible to control. Herbicides have significantly different impacts at different stages of a plant's growth and development. Likewise, not all biological control agents are effective in all habitats. For example, lantana has been contained in some areas by biological control agents but remains uncontrolled in others (Gardner and Davis 1982). The most important functions of research are to evaluate the role of weeds in island ecosystems, their impact on individual native species, their dependency upon disturbance for success, and management strategies.

Weed management needs much greater evaluation today than in the past. The indiscriminate use of herbicides is very dangerous, not only to human health but also to the well-being of the native ecosystems in which they are used. Agricultural weed control strategies are generally developed to eliminate all species other than the crop. In natural ecosystems we generally try to eliminate one species only and preserve the rest. In addition, we are ignorant of the longevity or secondary effects of herbicides in tropical areas because most chemicals are evaluated in temperate ecosystems. Also, weeds can develop resistance to herbicides

(Hanson 1956, 1962). This problem becomes more acute the longer the herbicide program is conducted. The temptation to use higher dosages, a very common practice in agriculture, must be assiduously avoided. Physical damage to the ecosystem almost always occurs during the application of the herbicide. However, a particular advantage of herbicide use is that the soil is left undisturbed, and in many instances the dead plant tissues form a ground cover that will impede the growth of seedlings.

Mechanical control is very expensive because it requires manpower. Another negative factor is the accompanying damage to the ecosystem in the process of weeding. The disturbance of the soil under the plant generally stimulates weed seeds to germinate.

Natural areas are not amenable to some techniques of weed control, e.g. changing cultural practices. However, the extent of the infestation or the sensitivity of the protected area may preclude any disturbance. In these instances, biological control is a potentially powerful weapon, but it is not a panacea (Howarth 1983; Mellanby 1974) and sometimes operates only in very restricted ranges. It is very expensive initially and the agents are not confined within any political boundaries.

Biological control is not the final solution to alien species problems in Hawai'i, yet some successes make it extremely attractive because it seems to be the natural solution to a problem. Although most species have other organisms that parasitize or feed on them, the successful introduction of these organisms is a formidable problem. Many may not be suitable for importation for the following reasons.

1. They may not be species specific. In general, this would automatically exclude a species, but there are instances where whole genera may be the target of a control program, e.g. *Melastoma*. However, as Harris (1973) and Pimentel (1963) point out, it may be better to look for biocontrol agents on closely related species because those specific to the target organism may be in a symbiotic balance.

2. They may themselves be parasitized by insects or fungi already present. It would not be appropriate to introduce a control agent that itself may be controlled to a level at which it is no longer effective.

3. The target species is related to sugar cane, pineapple or some other important agricultural crop. The possibility that a species introduced to control the relative may slip over to one of these important

agricultural crops would be enough to prohibit entry.

The situation could also be reversed where the relative may act as a reservoir for a pest of the crop. However, this approach has been carried too far in Hawai'i, where the sugar cane industry has resisted all efforts to import biological control agents against any grass. On the other hand, it is surprising that the pineapple industry has not objected to the continuing, almost uncontrolled, importation of bromeliads.

4. The ecological requirements of the agent may be found only in part of the target species range in the Islands, if at all.

5. The species may be controlled only by a number of organisms which affect different stages of the plant's life history. The problem is that as more species are introduced, the likelihood of secondary impacts increases. It is impossible to screen the potential agent against all native species. In fact, most agents are only evaluated against commercially important species and sometimes related or important native species.

6. The alien may not be controlled by herbivores or parasites but by succession in its native habitat. Many pests of tropical island ecosystems appear to be of this nature. They would not be amenable to biological control and would have to be controlled by other means.

7. Parasites of control agents may have been introduced earlier in relation to another problem. The early importation of general parasites of Lepidoptera may prevent the use of heliconiid butterflies as control agents of Passiflora in Hawai'i.

These last points are often misunderstood by many casual exponents of biological control. The problem is further complicated by the fact that problematic alien species generally infest their "fundamental" niche (Hutchinson 1957), having escaped many of the constraints which confined them to the "realized" niche of their native environment. Thus, a suitable biological control agent will probably only be effective in a segment of the insular range of the alien.

Biological control is a science wrapped up in a restrictive bureaucracy, but with good reason. At times the rules appear overly stifling, but they are necessary to prevent abuse and to adequately demonstrate the safety of the proposal. It is tragic that such rules are not applied to the importation of alien plants in the first place. That biological control is not a panacea is further emphasized by its expense and the time necessary to verify that an agent is not only suitable but reasonably certain not to have undesirable side effects. It is, therefore, initiated only after all else fails.

Thus, there is no easy answer to controlling alien plants in insular environments. Each species has to be managed on its own and generally by a number of different approaches. It is the successful integration of these different approaches that is the challenge to the research scientist and the manager. Solutions are not to be quickly found in most cases, but probably control is possible for most plants.

CONCLUSIONS

Introduced plants can be quite innocuous. For example, it is highly unlikely that such horticultural favorites as plumeria (*Plumeria acuminata* Ait.) or pua kenikeni (*Fagraea berteriana* Gray) will ever pose a threat to native ecosystems. On the other hand, a number of alien species, e.g. Koster's curse and strawberry guava, are very serious threats. My candidates for the 10 most serious weeds in Hawai'i, in order of priority, are: strawberry guava, Koster's curse, banana poka, fountaingrass, fayatree, kikuyugrass, Christmasberry, blackberry, molassesgrass, and bushbeardgrass.

It is generally believed that under natural conditions island ecosystems are stable, invasion-resistant assemblages of species whose combined resource exploitation is in balance with productivity (MacArthur 1972). Without other alien influences, island biogeographers and ecologists would predict that very few alien introductions would become established in native communities (Cockayne 1928; Allan 1936; Anderson 1952). However, island ecosystems are disturbed to varying degrees by man, fire, feral ungulates, introduced birds, and a vast array of alien invertebrates. In Hawai'i, a significant number of native species has become extinct due to alien influences. Thus the underlying ecological processes on which native communities are structured have changed, probably irreversibly, in most cases.

One problem facing managers of native ecosystems is the determination of the significance of negative impacts of alien plants in native ecological processes. If a weed does not affect, or only marginally affects, ecosystems, e.g., *Euphorbia hirta* L., then it can be tolerated. As the system recovers, such species will be contained. Species at the other end of the scale, e.g., strawberry guava, need immediate attention. The mechanism of entry and establishment of an alien in the ecosystem is very important. If a weed is dependent on disturbance, then control can focus on preventing such occurrences, where possible. However, if the weed is invasive, then management must attempt to reduce or eliminate the species. Probably no species is beyond control as long as time and money are available. However, political and practical considerations may preclude such optimism. Such considerations include whether: the target species is socially useful in some context; it is too closely related to a commercial crop species; its impact in a remote ecosystem is too unfamiliar to attract the necessary funding; or the control program interferes with the activities of a special interest group, such as hunters.

This paper identifies 86 alien plants which are serious weeds in Hawaiian ecosystems. All but one, Hypochoeris radicata, displace native species when growing in the same habitat. Twenty-six (30%) have, or are suspected of having, allelopathic activity against native species. Twelve (14%), principally grasses, are fire-enhanced species which invade the fire-disturbed area much faster than the natives. In so doing, they increase the fuel level in the ecosystem and carry fires over larger areas than before and generally at higher intensities. On the other hand, another 10 (12%) species are known to inhibit fires.

Just over half of the significant aliens, 45 (52%), are phanaerophytes, 18 (21%) chamaephytes, 10 (12%) hemicryotophytes, 6 (7%) lianes, 5 (6%) are geophytes, and 2 (2%) therophytes. The preponderance of trees, particularly evergreen species, is of considerable concern because they become an integral part of the canopy. Here they have a much greater disruptive influence on ecological processes. The large number of vines, all of them photophilic canopy species, is particularly important in Hawai'i where this growth form is poorly represented in the flora and, until recently, not a significant feature in the ecosystem. Thus, instead of being a natural part of succession as in other tropical areas, they destroy the forest structure by shading or breaking native tree branches.

Seventy-five percent of the weed species are well-adapted for dispersal in the Islands. Thirty (35%) are dispersed by predominantly alien, frugivorous birds, 29 (34%) by wind, and 9 (10%) on clothing or animal hides. One species is dispersed by water. However, it is somewhat surprising that 23 (27%) are dispersed only by man in the Islands. Once established, their infestation intensifies with some local dispersal by physical means.

Forty-five (52%) species are confined to the highly altered lowland (below 800 m) ecosystems, 10

(12%) range from sea level to mid-elevations (between 800-1,700 m), 18 (21%) are principally confined to mid-elevations, 3 (3%) to both mid- and higher elevations (up to 2,700 m), and 10 (12%) are confined to the higher elevations. The preponderance of pests in the lowlands is expected due to the extent and variety of disturbance there, as well as the increased opportunity for introduction.

Most of the weeds presented in this listing invade native communities only after some type of disturbance, generally the consequence of man but occasionally natural, e.g., landslides, hurricanes, and treefalls. However, approximately half of the species listed (particularly those dispersed by wind or birds) can invade native ecosystems but generally remain minor components until some disturbance occurs. Twenty-three species have the ability to invade and take over native ecosystems without any apparent disturbance. These are: African tuliptree, Ardisia, banana poka, blackberry, bush beardgrass, Christmasberry, fiddlewood, fountaingrass, glorybush, huehue-haole, Indian fleabane, Indian rhododendron, juniperberry, kahili ginger, Koster's curse, lantana, melochia, miconia, raspberry, roseapple, rosemyrtle, strawberry guava, and yellow Himalayan raspberry.

Egler (1942) suggested that weeds, such as koa haole, would ameliorate ravaged native ecosystems, allowing native species to reestablish themselves. Unfortunately, the time frame about which he was talking is so long that many natives would already be extirpated before conditions were favorable. Very few native species are able to maintain themselves in heavy infestations of arborescent weeds. Those that do are generally so weakened that seed production is severely diminished or absent. However, the critical weakness is that the native species cannot compete against the aliens in the germinant and early seedling stages. The outcome is that the seedbank of native species is exhausted, effectively excluding the species from that area; reinvasion would be the only means of reestablishment. Since weeds normally occupy all the available space in the habitat, the prognosis for the native species is dismal. Overall, it is almost hopeless because succession, if it occurs at all, is generally by alien species. One weed is replaced by another; in the case of koa haole, Christmasberry and Java plum are frequent invaders of the habitat. The native species are therefore still excluded.

With the exception of St. Helena and Madagascar, the Hawaiian Islands contain the most ravaged island ecosystems in the world. The introduction of more than 4,600 different plants can only have a devastating effect on the survival of the 1,700+ native species.

It is fortunate that less than 100 aliens have become pests. However, that number will increase continuously if restrictions are not imposed. It is because of such considerations that it is imperative that the importation of alien plants be stopped and the continued disturbance of native ecosystems prevented.

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LITERATURE CITED

Achhireddy, N.R., and M. Singh. In press. Allelopathic effects of lantana (*Lantana camara*) on milkweed vine (*Morrenia odorata*). *Weed Sci.* 32.

Allan, H.H. 1936. Indigene versus alien in the New Zealand plant world. *Ecology* 17:187-193.

Amerson, A.B., Jr. 1971. *The natural history of French Frigate Shoals, Northwestern Hawaiian Islands.* Atoll Res. Bull. 150.

Amerson, A.B., Jr., R.B. Clapp, and W.O. Wirts II. 1974. *The natural history of Pearl and Hermes Reef, Northwestern Hawaiian Islands.* Atoll Res. Bull. 174.

Anderson, E. 1952. *Plants, man and life*. Berkeley, Calif.: Univ. Calif. Pr.

Baker, J.K., and D.W. Reeser. 1972. *Goat management problems in Hawaii Volcanoes National Park: a history, analysis, and management plan*. Natl. Park Serv. Nat. Resour. Rep. 2.

Bradshaw, A.D., M.J. Chadwick, D. Jowett, and R.W. Snaydon. 1964. Experimental investigations into the mineral nutrition of several grass species: IV. Nitrogen level. *J. Ecol.* 52:665-676.

Carlquist, S. 1965. *Island life. A natural history of the islands of the world*. New York: Nat. Hist. Pr.

Chou, C.H., and C.C. Young. 1975. Phytotoxic substances in twelve subtropical grasses. *J. Chem. Ecol.* 1: 183-193.

Clapp, R.B., and F.C. Silbey. 1971. *Notes on the vascular flora and terrestrial vertebrates of Caroline Atoll, Southern Line Islands.* Atoll Res. Bull. 145.

Clapp, R.B., and W.O. Wirtz, II. 1975. *The natural history of Lisianski Island, Northwestern Hawaiian Islands.* Atoll Res. Bull. 186.

Clapp, R.B., E. Kridler, and R.R. Fleet. 1977. *The natural history of Nihoa Island, Northwestern Hawaiian Islands.* Atoll Res. Bull. 207.

Cockayne, L. 1928. *The vegetation of New Zealand.* Weinheim, New Zealand: H.R. Engelmann.

Crawford, R.M.M. 1983. Root survival in flooded soils. In Ecosystems of the world. 4A. Mires, swamps, bog, fen and moor: general studies, ed. A.J.P. Gore, 257-283. Amsterdam: Elsevier Sci. Pub. Co.

Diong, C.H. 1983. Population ecology and management of the feral pig (Sus scrofa L.) in Kipahulu Valley, Haleakala National Park, Maui, Hawaii. Ph.D. Diss., Univ. Hawaii, Honolulu.

Duffey, E. 1964. The terrestrial ecology of Ascension Island. J. Appl. Ecol. 1:219-251.

Egler, F.E. 1942. Indigene versus alien in the development of arid Hawaiian vegetation. Ecology 23:14-23.

Ely, C.A., and R.B. Clapp. 1973. The natural history of Laysan Island, Northwestern Hawaiian Islands. Atoll Res. Bull. 171.

Feare, C.J. 1979. Ecological observations on African Banks, Amirantes. Atoll Res. Bull. 227.

Fosberg, F.R. 1948. Derivation of the flora of the Hawaiian Islands. In Insects of Hawaii, ed. E.C. Zimmerman, Vol. 1, Introduction, 107-119. Honolulu: Univ. Hawaii Pr.

Fosberg, F.R. 1953. Vegetation of Central Pacific atolls, a brief summary. Atoll Res. Bull. 23.

Gardner, D.E. 1984. Kikuyu grass rust caused by Phakopsora apoda in Hawaii. Plant Dis. 68:826.

Gardner, D.E., and C.J. Davis. 1982. The prospects for biological control of nonnative plants in Hawaiian national parks. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. 48. Honolulu: Univ. Hawaii.

Gardner, D.E., and V.A.D. Kageler. 1983. Glyphosate in the control of kikuyugrass, and its effects on associated native and nonnative plants in Hawaiian national parks. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. 49. Honolulu: Univ. Hawaii.

Gerrish, G. and D. Mueller-Dombois. 1980. Behavior of native and non-native plants in two tropical rain forests on Oahu, Hawaiian Islands. Phytocoenologia 8:237-295.

Gogue, G.J., C.J. Hurst, and L. Bancroft. 1974. Growth inhibition by Schinus terebinthifolius. Am. Soc. Hort. Sci. 9:45.

Hanson, N.S. 1956. Dalapon for control of grasses on Hawaiian sugar cane lands. Down to Earth 12:2-5.

Hanson, N.S. 1962. Weed control practices and research for sugar cane in Hawaii. Weeds 10:192-200.

Harper, J.L. 1965. Establishment, aggression, and cohabitation in weedy species. In The genetics of colonizing species , ed. H.G. Baker and G.L. Stebbins, 243-265. New York: Academic Pr.

Harris, D.R. 1962. Invasion of oceanic islands by alien plants. Inst. Brit. Geogr. Trans. 31:67-82.

Harris, D.R. 1965. Plants, animals and man in the outer Leeward Islands. Univ. Calif. Pub. Geogr. 18.

Harris, P. 1973. The selection of effective agents for the biological control of weeds. Proc. 3rd Internatl. Symp. Biol. Contr. Weeds, 75-85. Montpelier, France.

Haselwood, E.L., and G.G. Motter. 1983. Handbook of Hawaiian weeds. 2nd ed. Honolulu: Univ. Hawaii Pr.

Hedburg, O. 1951. Vegetation belts of the East-African Mountains. Svensk Bot. Tidsk. 45:140-202.

Higgs, D.E.B., and D.B. James. 1969. Comparative studies on the biology of upland grasses: I. Rate of dry matter production and its control in four grass species. J. Ecol. 57:553-563.

Hosaka, E.Y. 1958. Kikuyugrass in Hawaii. Univ. Hawaii Agric. Ext. Serv. Circ. 389.

Hosaka, E.Y., and A. Thistle. 1954. Noxious plants of the Hawaiian ranges. Univ. Hawaii Coop. Ext. Serv. Bull. 62.

Howarth, F.G. 1983. Classical biocontrol: panacea or Pandora's box. Proc. Hawaii. Entomol. Soc. 24 (2&3):239-244.

Humbert, G. 1927. La destruction d'une flore insulaire par le feu. Acad. Malagache Mem. V.

Hutchinson, Q.E. 1957. Concluding remarks. Cold Spring Harbor 22nd Symp. Quant. Biol., 415-427.

Jacobi, J.D. 1981. Vegetation changes in a subalpine grassland in Hawaii following disturbance by feral pigs. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. 41. Honolulu: Univ. Hawaii.

Judd, C.S. 1936. Seed dispersal in Hawaii. Mid. Pac. Mag. 49:111-118.

Kirch, P.V. 1982. The impact of the prehistoric Polynesians on the Hawaiian ecosystem. Pac. Sci. 36:1-14.

Krajina, V.J. 1963. Biogeoclimatic zones of the Hawaiian Islands. Hawaii. Bot. Soc. Newsl. 2: 93-98.

Lamoureux, C.H. 1963. The flora and vegetation of Laysan Island. Atoll Res. Bull. 97.

La Rosa, A.M. 1983. The biology and ecology of Passiflora mollissima in Hawaii. M.S. Thesis, Univ. Hawaii, Honolulu.

Lee, M.A.B. 1974. Distribution of native and invader plant species on the island of Guam. Biotropica 6:158-164.

Loveless, A.R. 1960. The vegetation of Antigua, West Indies. J. Ecol. 48:495-527.

MacArthur, R.H. 1972. Geographical ecology: patterns in the distribution of species. New York: Harper and Row.

Mahmoud, A., and J.P. Grime. 1976. An analysis of competitive ability in three perennial grasses. New Phytol. 77:431-435.

Markin, G.P. 1984. Biological control of the noxious weed gorse Ulex europaeus L.: a status report. Proc. 5th Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 77. Honolulu: Univ. Hawaii.

Martin, P., and B. Rademacher. 1960. Studies on the mutual influences of weeds and crops. In The biology of weeds, ed. J.L. Harper, 143-152. Oxford, England: Blackwell Sci. Pub.

Mellanby, K. 1974. The future of biological control in Britain: a conservationist's view. In Biology in pest and disease control, ed. D. Price-Jones and M.E. Solomon, 349-353. Oxford, England: Blackwell Sci. Pub.

Melville, R. 1979. Endangered island floras. In Plants and Islands, ed. D. Bramwell, 361-378. London: Academic Pr.

Mian, S., G. Bond, and C. Rodrigues-Barrueco. 1976. Effective and ineffective root nodules in Myrica faya. Proc. Royal Soc. Lond., Ser. B, 194:285-293.

Miguel, C., and C. Rodrigues-Barrueco. 1974. Acetylene-reducing activity of detached root nodules of Myrica faya Ait. Plant and Soil 41:521-526.

Mueller-Dombois, D. 1973. A non-adapted vegetation interferes with water removal in a tropical rain forest area in Hawaii. Trop. Ecol. 14:1-18.

Mueller-Dombois, D. 1981. Understanding Hawaiian forest ecosystems: the key to biological conservation. In Island ecosystems: biological organization in selected Hawaiian communities, ed. D. Mueller-Dombois, K.W. Bridges, and H.L. Carson, 502-520. Stroudsburg, Penn.: Hutchinson Ross Pub. Co.

Mune, T.L., and J.W. Parham. 1967. The declared noxious weeds of Fiji and their control. Fiji Dep. Agric. Bull. 48.

Nakahara, L.M., and P.Y. Lai. 1984. New state record ... Psyllids. Hawaii Pest Rep. 4:2-9.

Neal, M.C. 1965. In gardens of Hawaii. B.P. Bishop Mus. Spec. Pub. 50.

Norton, G.A., and G.R. Conway. 1977. The economic and social context of pest disease and weed problems. In Origins of pest, parasite, disease and weed problems, ed. J.M. Cherrett and G.R. Sapar, 205-226. Oxford, England: Blackwell Sci. Pub.

Pimentel, D. 1963. Introducing parasites and predators to control native plants. Can. Entomol. 95: 785-792.

Plucknett, D.L., and B.C. Stone. 1961. The principal weedy Melastomaceae in Hawaii. Pac. Sci. 15: 301-303.

Rauh, W. 1979. Problems of biological conservation in Madagascar. In Plants and islands, ed. D. Bramwell, 405-422. London: Academic Pr.

Rice, E.L. 1972. Allelopathic effects of Andropogon virginicus and its persistence in old fields. Am. J. Bot. 59:752-755.

Ripperton, J.C., and E.Y. Hosaka. 1942. Vegetation zones of Hawaii. Hawaii Agric. Exp. Stn. Bull. 89.

Rorison, I.H. 1968. The response to phosphorus of some ecologically distinct plant species: I. Growth rates and phosphorus absorption. New Phytol. 67: 913-923.

St. John, H. 1973. List and summary of the flowering plants in the Hawaiian Islands. Pac. Trop. Bot. Gard. Mem. 1.

St. John, H. 1978. The first collection of Hawaiian plants by David Nelson in 1779. Hawaiian plant studies 55. Pac. Sci. 32:315-324.

Salisbury, E. 1964. Weeds and aliens. 2nd ed. London: Collins.

Sanchez, J., and F. Davis. 1969. Growth inhibitors in kikuyu (Pennisetum clandestinum) as factors of its competitive ability. [Abstract] I Semm. Soc. Colomb. de Contr. des Malezas y Fisiol. Vegetal (COMALES), 23-24, 58-59.

Sauer, J.D. 1982. Cayman Island seashore vegetation: a study in comparative biogeography. Univ. Calif. Pub. Geogr., Vol. 25.

Simmonds, H.W. 1933. The biological control of the weed Clidemia hirta D. Don. in Fiji. Entomol. Res. Bull. 24:345-348.

Simpson, B.B., ed. 1977. Mesquite: its biology in two desert scrub ecosystems. U.S. Internatl. Biol. Prog. Synth. Ser. 4. Stroudsburg, Penn.: Dowden, Hutchinson and Ross.

Smith, C.W., T. Parman and K. Wampler. 1980. Impact of fire in a tropical submontane seasonal forest. In Proc. 2nd Conf. Sci. Res. Natl. Parks. Vol. 10, Fire Ecology, 313-324. San Francisco, Calif.: Natl. Park Serv.

Sorensen, J.C. 1980. Phenology of Andropogon virginicus in Hawaii. M.S. Thesis, Univ. Hawaii, Honolulu.

Spicer, R.A., and D. Mc. Newbery. 1979. The terrestrial vegetation of an Indian Ocean coral island: Wilingili, Addu Atoll, Maldive Islands. 1. Transect analysis of the vegetation. Atoll Res. Bull. 231.

Stoddart, D.R. 1967. Summary of the ecology of coral islands north of Madagascar (excluding Aldabra). In Ecology of Aldabra Atoll, Indian Ocean, ed. D.R. Stoddart, 53-62. Atoll Res. Bull. 118.

Stoddart, D.R. 1971. Land Vegetation of Diego Garcia. In Geography and ecology of Diego Garcia Atoll, Chagos Archipelago., ed. D.R. Stoddart and J.D. Taylor, 127-142. Atoll Res. Bull. 149.

Stoddart, D.R., and F.R. Fosberg. 1981a. Bird and Dennis Islands, Seychelles. Atoll Res. Bull. 252.

Stoddart, D.R., and F.R. Fosberg. 1981. Topographic and floristic change, Dry Tortugas, Florida 1904-1977. Atoll Res. Bull. 253.

Stoddart, D.R., and C.A. Wright. 1967. Geography and ecology of Aldabra Atoll. In Ecology of Aldabra Atoll, Indian Ocean., ed. D.R. Stoddart, 11-52. Atoll Res. Bull. 118.

Stoddart, D.R., P.E. Gibbs, and D. Hopley. 1981. Natural history of Raine Island, Great Barrier Reef. Atoll Res. Bull. 254.

Stone, C.P. Alien animals in Hawaii's native ecosystems: toward controlling the adverse effects of introduced vertebrates. [This volume]

van der Werff, H. 1979. Conservation and vegetation of the Galapagos Islands. In Plants and Islands, ed. D. Bramwell, 391-404. London: Academic Pr.

Vogl, R.J. 1969. The role of fire in the evolution of the Hawaiian flora and vegetation. Proc. Ann. Tall Timbers Fire Ecol. Conf., April 1969, 5-60. Tallahassee.

Wace, N.M. 1966. The last of the virgin islands. Discovery 27:36-42.

Warshauer, F.R., J.D. Jacobi, A.M. La Rosa, J.M. Scott, and C.W. Smith. 1983. The distribution, impact and potential management of the introduced vine Passiflora mollissima (Passifloraceae) in Hawaii. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. 48. Honolulu: Univ. Hawaii.

Watt, T.A. 1978. The biology of Holcus lanatus L. (Yorkshire fog) and its significance in grassland. Herbage Abstracts 48:195-204.

Watts, D. 1970. Persistence and change in the vegetation of oceanic islands. Can. Geogr. 14: 91-109.

Wester, L.L., and H.B. Wood. 1977. Koster's curse (*Clidemia hirta*), a weed pest in Hawaiian forests. *Environ. Conserv*. 4:35-41.

Whelan, B.R., and D.G. Edwards. 1975. Uptake of potassium by *Setaria anceps* and *Macroptilium atropurpureum* from the same standard solution culture. *Austral. J. Agric. Res.* 26:819-829.

Whistler, W.A. In press. *Weed handbook for Western Polynesia.* Eschborn, W. Germany: Geselischafr fur Techniche Zussamznarbeit.

Woodward, P.W. 1972. *The natural history of Kure Atoll, Northwestern Hawaiian Islands*. Atoll Res. Bull. 164.

9.

ALIEN ANIMALS IN HAWAI'I'S NATIVE ECOSYSTEMS: TOWARD CONTROLLING THE ADVERSE EFFECTS OF INTRODUCED VERTEBRATES

Charles P. Stone

ABSTRACT

The adverse effects of introduced birds and mammals on native taxa and ecosystems in Hawai'i have been long term, widespread, and severe. Impacts began at least 1,500 years ago with colonization by the Polynesians and their flora and fauna, and continued with their increasingly severe disturbance to the landscape, especially below 500 m elevation. Problems accelerated with the arrival of continental man in 1778, and continue to the present day with suspected deliberate releases of birds that threaten native species as recently as 1982. Alien vertebrates can affect native biota through predation, competition, depredation, and habitat degradation. Negative impacts can be subtle or dramatic, but evidence of importance is manifested in large percentages of extinct and rare taxa. In this paper, adverse effects of major bird and mammal introductions are outlined where possible for islands, vegetation zones, and rare taxa. Although much remains to be learned, suggestions for reducing negative effects of alien vertebrates can be made. These include: Enforcement of efficient quarantine procedures; sufficient support for enduring and complete vertebrate damage control programs (including research, management, and monitoring) on lands managed for preservation of native Hawaiian ecosystems and taxa; development of multiple and adaptable methods of vertebrate damage reduction; preservation and management of the most intact areas remaining in Hawai'i; and cooperation and communication among the agencies and special interest groups (including developers and conservationists) in land use planning on regional bases. Cooperative approaches, effective education and communication about the value of protected areas, and the increased usefulness of such areas for all citizens, are seen as particularly important in reducing continued damage to Hawai'i's remaining native ecosystems by alien vertebrates.

INTRODUCTION

Adverse effects of introduced or alien vertebrates on native Hawaiian ecosystems and organisms may be divided into 2 categories: those that occurred largely in the past (including the introductions of the early Polynesians), and those that occur at present. The first are of interest because they provide examples of the devastating effects that aliens can cause over time to native species with small population sizes and inadequate defenses against intruders. Such early disruptions, when viewed in accurately constructed and comprehensive historical contexts, can provide insights into compositions and functions of the Hawaiian biota at a time when it was more intact. The effects of past introductions also provide sufficient warning to provoke caution about future introductions or translocations. The adverse impacts of some of these introductions are unknown, but the effects of others are clearly visible today.

Ongoing and active disturbances by alien vertebrates are of interest for 2 additional reasons. First, they allow direct observation and manipulation through which one can obtain understandings of the ecology of aliens and interrelationships within ecosystems. Secondly, through reduction, exclusion, or elimination of problem animals, entire ecosystems (or important components thereof) can be rehabilitated to some degree (see Lamoureux, this volume). Where ecosystem deterioration caused by introduced animals can be stopped or slowed, systems may at least function with primarily native components; and natural processes (including nutrient cycling, gene flow, succession, and evolution), although not pristine, may also be less influenced by man and his induced changes.

Damage caused by alien vertebrates to native flora and fauna in Hawai'i may be categorized as predation, competition, depredation, or habitat degradation. Predation is the killing of one animal by another, and includes such important examples as the eating of eggs and young of birds by mammals, and consumption of insects and snails by mammals or birds. Competition is the negative influence of one animal on another when a resource needed by both is somehow limited. Relationships among native and exotic birds and a common food supply, and relationships among native birds, introduced rats and common food or nest sites, are examples. Depredation is the eating or otherwise destroying of plants by animals. Consumption, trampling, or uprooting of native plants (or plant parts) by alien mammals are examples. Depredations on plants influence other animals through impacts on their habitats, and these will be discussed under "Habitat Degradation."

Introduced vertebrates can have additional, subtle effects on native ecosystems and biota. Disease can be transmitted to native species through alien vertebrate reservoirs (see van Riper and van Riper, this volume). Introduced animals can disperse alien plants and thus increase plant densities, rates of spread, and distributional limits. Vertebrates sometimes also enhance germination of introduced plants through seed scarification in digestive tracts, or through digging up and/or fertilization with feces of potential seedbeds. Serious long-term damage can be caused by some alien vertebrates that disrupt nutrient cycling, initiate and accelerate erosion, radically change compositions of plant and animal communities, and alter evolution of other species through disruption of natural selection.

The purpose of this paper is to address some of the complexities of damage caused to native terrestrial ecosystems by birds and mammals introduced to Hawai'i by man. Introduced reptiles and amphibians also affect native species, particularly invertebrates (Howarth, this volume), but there is little information available about what are probably less severe impacts, at least currently. A brief summary of adverse effects prior to the arrival of European man will be presented, and the distribution of different kinds of impacts will be outlined by island and by general vegetation type. Management strategies for different animals and situations will be discussed and research needs identified. A coordinated approach to the management and research of introduced mammals and birds in Hawai'i's threatened ecosystems will be suggested.

POLYNESIAN IMPACTS (400 A.D. -- 1778 A.D.)

Beginning at least in 400 A.D., human colonizers of the Hawaiian Islands began arriving with their attendant land use practices, flora, and fauna. Vertebrate introductions included domestic pigs (Sus scrofa), red junglefowl (Gallus gallus), dogs (Canis familiaris), Polynesian or Pacific rats (Rattus exulans), and various stowaway reptiles (Kirch 1982). Although documentation is lacking, rats probably began to affect lowland invertebrates and plants shortly after human arrival; predation on low- or ground-nesting forest birds and seabirds would not be unexpected based on similar activity in historical time (Kepler 1967; Atkinson 1977; Imber 1978). Junglefowl, rats, and the other small vertebrates spread into lowland forests at rates dependent mostly upon genetic and behavioral adaptation to changing Hawaiian environments. High reproductive rates, low predation, and shortage of competition may have favored these small vertebrates in suitable habitat, especially that modified by man. However, on the whole, the continuing land modification by the early Hawaiians must have overwhelmed any effects of their introduced animals on the biota (Kirch 1982).

According to one estimate, about 80 percent of the lowland forest (below 500 m) was drastically altered by widespread use of fire, by agricultural and aquacultural development, and by forest clearing (Kirch 1982). Evidence of agriculture has been found as high as 1200 m in elevation (McEldowney 1983), and slash and burn agriculture was perhaps used to maintain pili grasslands (Kirch 1982) for thatching huts; Sadleria spp. and arrowroot (Tacca leontopetaloides) were used as pig fodder and famine food (McEldowney 1983). Descriptions of the early landscape were given by European explorers such as Cook and King, Vancouver and Menzies, and Chamisso (Olson and James 1982), and the impacts of Hawaiians on native vegetation are usually inferred from this.

A human population of perhaps 200,000-250,000 at the time of European contact (Schmitt 1971) may represent a decline resulting from reduced carrying capacity (Kirch 1982). The effects of such large numbers of people and their alterations of the native vegetation were undoubtedly large. Impacts on avian species alone were enormous, with 39 [now 45] of Hawai'i's 80 [now 86] known species of birds eliminated prior to the arrival of Western man in 1778 (Olson and James 1982). Most of the 13-15 flightless species of birds were probably hunted to varying degrees and eventually extirpated. Development of irrigated fields may have resulted in larger populations of the endemic Hawaiian duck (Anas wyvilliana), common moorhen (Gallinula chloropus), American coot (Fulica americana) and black-necked stilt (Himantopus mexicanus) as residents. Establishment of the short-eared owl (Asio flammeus) may have been aided by man's introduction of the Polynesian rat (Olson and James 1982).

Dogs and pigs were valued by Hawaiians as scavengers and as sources of animal protein (Handy and Handy 1972; Kirch 1979), and were probably usually kept under control. Junglefowl and their eggs may have been less favored for food (Handy and Handy 1972) than some other sources, and may therefore have been less controlled; they formerly ranged from sea level to 2,100 m on Hawai'i (Schwartz and Schwartz 1949). Junglefowl also may have arrived later than other domestics (Tuggle 1979), but this is uncertain. Handy and Handy (1972) noted that pigs were allowed to "run about the kauhale (homestead) and gardens while they were young, but when they were sizable and ready for fattening they were penned inside enclosures of heaped-up stones." Whether this was always the case is unknown. Recent evidence suggests that pigs sometimes were separated from gardens and irrigated fields by keeping them within village walls (D.B. Barrere, pers. comm.). Pigs probably existed throughout most of the islands by the time of European contact (McEldowney 1979), and feral populations in "moist" forests could have been "an older utilized resource" (McEldowney 1983). Whether they were important invaders of Hawaiian rain forests is unknown. As on other Pacific islands such as New Guinea, some pigs may have been tightly managed and herded with dogs; some may have been caught at times from nearby forests and fallow fields; and some may have been semi-wild or pariah (Diong 1983) populations, fed and even called in by people as needed (H. McEldowney, pers. comm.).

The reportedly small size of Polynesian pigs may have been less a function of genetics than a diet low in protein and the rapid use of younger pigs for food. P.V. Kirch (pers. comm.) noted that most pigs recovered from archaeological sites are young and that pigs were fed coconut, sweet potato, and breadfruit. Pigs also ate human wastes and thus served as a means of village sanitation. Handy and Handy (1972) suggested that feral pigs in upland areas subsisted on fruits, nuts, seeds, and various ferns, and that they "grubbed for roots." Considerable acreages of fallow land and secondary growth (McEldowney 1983) may have served to attract foraging feral pigs more than dense rain forest.

Animal protein is required for maximum growth and reproduction of pigs (Pond and Houpt 1978; National Research Council 1979), and other than turtle eggs, fish, and beached marine mammals from a sometimes capricious ocean, there were few protein sources in native, as opposed to man-influenced, ecosystems. (Animal protein may have declined as human populations increased, as it has elsewhere, e.g. Kirch and Yen 1982.) Thus, feral pig populations that existed in rain forests prior to Cook's arrival may have been comprised of small-sized pigs at low densities. What is known about nutrition, pig husbandry practices, and agricultural land use would seem to suggest that modifications of the interior rain forest vegetation by Polynesian pigs was not great.

EFFECTS ON ISLANDS AND ECOSYSTEMS

Although Polynesian introductions and land use resulted in changes that continue to the present day, subsequent deliberate and accidental introductions and practices of early explorers, settlers, agriculturists, hunting groups, bird clubs, and governments caused additional modifications. More comprehensive histories of vertebrate introductions and distributions are given elsewhere (Tomich 1969; Kramer 1971; van Riper and van Riper 1982; Berger 1974, 1975, 1981), and will not be repeated here.

The effects of the alien vertebrates now present are complex, varied, and subtle. Some of the direct effects on different vegetational types and the biota of the Hawaiian Islands will be mentioned in this section. As indicated earlier, the general headings will be depredation, predation, competition, and habitat degradation. A complete treatment is not possible, but what is considered most important will be stressed. Illustrations of indirect effects and of the complexities involved in reducing alien influences will then be presented. More succinct statements about problems and ongoing and proposed solutions will be found in a subsequent section. A diagram of general impact of important vertebrate taxa is presented in fig. 1 (after Scott et al., in press). A much condensed table of rare plant taxa threatened by alien vertebrates (table 1) was adapted from the more complete treatment by Wagner, Herbst, and Yee (this volume).

Depredation

Domestic and feral cattle (*Bos taurus*). Cattle were "historically abundant on Kauai, Oahu, Molokai, Maui, and Hawaii" and heavily overstocked on Lana'i (Tomich 1969). Feral cattle were eliminated by the mid 1900's on O'ahu, and probably Moloka'i more recently, but still exist on Maui (L.L. Loope, pers. comm.) and Hawai'i. Present distribution on Hawai'i includes the South Kona District, Mauna Loa, and Hamakua and Puna forests. Cattle are present in remote forests, in subalpine scrub, or on inaccessible lava flows on ranchlands (Tomich 1969; R.L. Walker, pers. comm.).

These animals have serious negative impacts on the vegetation of dry, mesic, and wet forests at low and high elevations. According to Scott et al. (in press):

> Domestic and feral cattle have been overall the single most destructive agent to Hawaiian ecosystems, particularly to mesic forests.... Koa reproduction is completely suppressed by grazing (Baldwin and Fagerlund 1943), and cattle are mostly responsible for converting large tracts of forest to open pasture on south and northwest Haleakala, lower elevations of west Maui and Lanai, much of Molokai, the dry side of Kohala Mountain..., the Waimea plains, the north side of Mauna Loa below 2200 m elevation, the mesic and west slopes of Hualalai, most of south

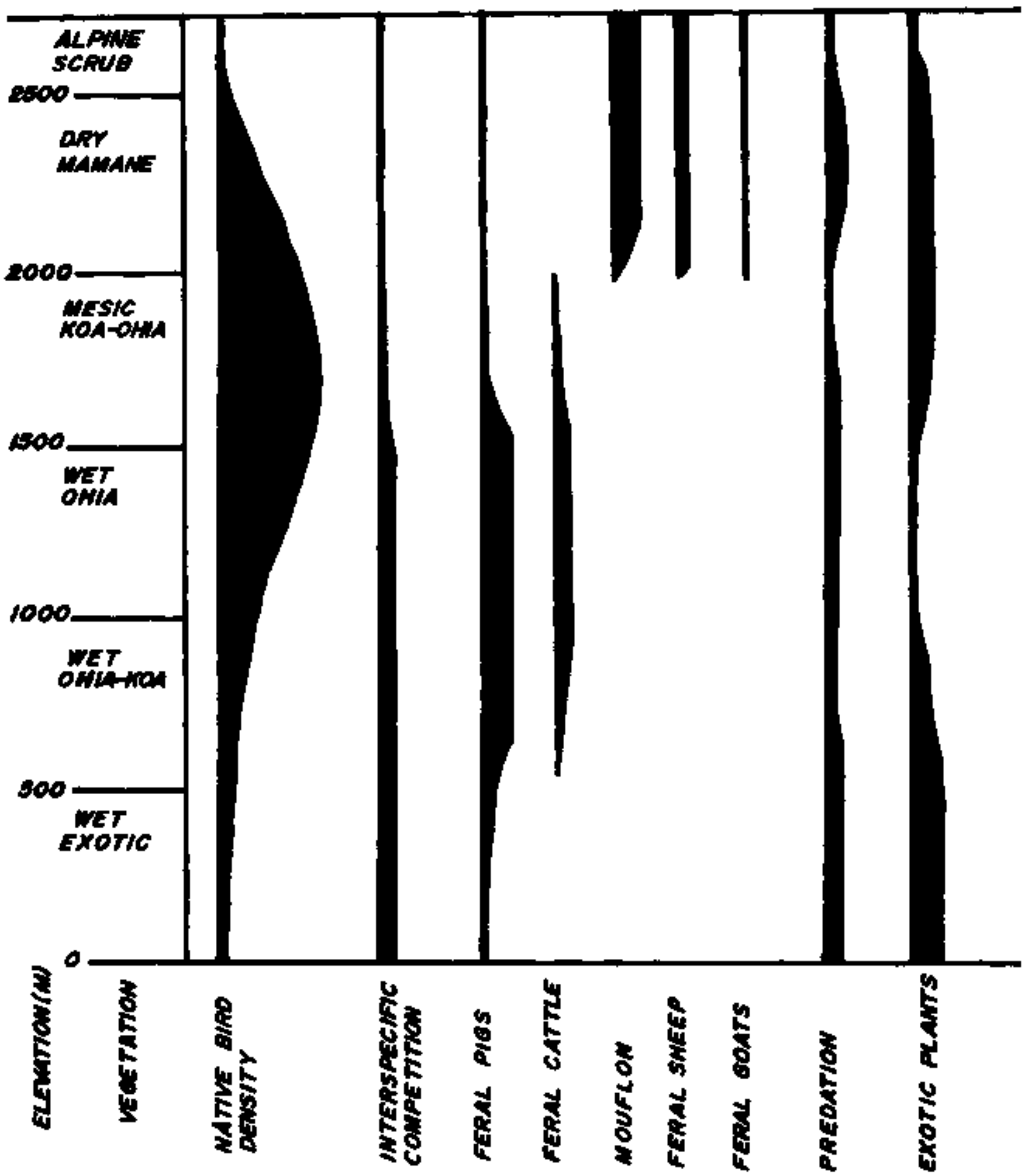

Figure 1. Stresses on native bird populations in Hawai'i (adapted from Scott et al., in press).

Table 1. Native Hawaiian plants listed as endangered (L), proposed for listing (P), or candidates for review by the U.S. Fish and Wildlife Service (C), that are also thought to be harmed by alien vertebrates.[1]

Taxon	Distribution[2]	Status	Threats[3]
Haplostachys haplostachya var. angustifolia	H	L	Feral goats, sheep, fire, alien plants, military
Vicia menziesii	H	L	Cattle, logging, pigs, reforestation, rodents
Gouania hillebrandi	M	L	Feral and domestic livestock, alien plants, insects
Kokia drynarioides	H	L	Livestock, fountain grass, rodents, fire
Abutilon menziesii	H,L	C	Axis deer, cattle, goats, insects, fire
Argyroxiphium sandwicense var. sandwicense	H	C	Feral animals, especially mouflon; removal of fruit for propagation
Cyanea superba	O	C	Feral cattle, goats, pigs, alien plants, fire, military

Taxon	Distribution[2]	Status	Threats[3]
Gardenia brighamii	O,Mo,L,M,H	C	Introduced herbivores, fire, agriculture, alien plants, rodents,insects
Hibiscadelphus distans	K	C	Feral goats, vandalism, fire, rats, insects
Mezoneuron kavaiense	K,O,M,H	C	Domestic and feral animals, alien plants, rodents, fire, wood harvest, insects
Remya mauiensis	M	C	Feral and domestic animals
Santalum freycinetianum var. lanaiense	L,M	C	Domestic and feral animals, agriculture, alien plants, rats

1 Adapted from Wagner, Herbst, and Yee (this volume).
2 Hawai`i, Lana`i, O`ahu, Moloka`i, Maui, Kaua`i.
3 Botanists can also threaten some species.

Kona, and the slopes between Mauna Kea and Kilauea. A consistent pattern of cattle invading wet forests from adjacent mesic areas occurs at ecotones on Maui and Hawaii, and formerly occurred on Kauai before control in the 1920's to 1930's...

Cattle were involved (with goats and sheep) in removing much of the native dryland forest on Ni'ihau and Kaho'olawe (Wagner, Herbst, and Yee, this volume). They have severely reduced mamane (Sophora chrysophylla) trees on Parker Ranch on Hawai'i (Scowcroft 1983). McEldowney (1983) summarized some of the drastic impacts on vegetation, soil and water supplies in the Waimea area in the mid to late 1800's but suggested that the native forests were reduced by Hawaiian land use practices as well as cattle depredations.

In addition to causing forest destruction and fragmentation, cattle have seriously threatened and probably caused the extinction of many native plant taxa. Cattle currently threaten rare plants such as Vicia menziesii, Abutilon menziesii, and Cyanea superba (table 1). Cattle reduce native plant diversity and simplify structure, composition, and function of vegetation near the ground. The effects of severe grazing pressure on plant gene pools, nutrient cycling, and, plant evolution (through natural selection) are undoubtedly severe.

Feral sheep (Ovis aries). This species occurs from 600-3,600 m on Hawai'i. It is present chiefly on Mauna Kea and Hualalai, although it descends to sea level in the Ka'u District (Tomich 1969; van Riper and van Riper 1982). Feral sheep have not been seen on Kaho'olawe since the early 1980's (R.L. Walker, pers. comm.).

Sheep mainly damage dry areas above 1,000 m on Hawai'i. Their effects on mamane reproduction can be extreme, especially near tree line (van Riper 1980; Scowcroft 1983; Scowcroft and Giffin 1983). Feral sheep compact soil and increase erosion through establishment and repeated use of trails. Sheep were implicated with goats and cattle in the destruction of much of the native vegetation of Ni'ihau and Kaho'olawe (Wagner, Herbst, and Yee, this volume). Feral sheep are a threat to the Federally endangered Haplostachys haplostachya var. angustifolia, (table 1), Mauna Kea silversword (Argyroxiphium sandwicense var. sandwicense), Stenogyne diffusa, S. microphylla, and probably other rare taxa in Hawai'i's dry uplands.

Mouflon (Ovis musimon). Mouflon are established on upper Mauna Loa and Mauna Kea on Hawai'i, and in the dry kiawe (Prosopis chilensis) forests of Lana'i (Tomich 1969; van Riper and van Riper 1982). In the mamane forests of Mauna Kea, they have effects on the vegetation similar to those of feral sheep (Giffin 1982). In subalpine 'ohi'a (Metrosideros polymorpha) and alpine scrub in the Ka'u District on Hawai'i, they also damage Ka'u silversword (Argyroxiphium kauense) and other native plants; on Mauna Kea, they threaten A. sandwicense var. sandwicense. On Lana'i, mouflon apparently do not penetrate native forest (Scott et al., in press).

Feral goats (Capra hircus). Goats in Hawai'i now occur on all main islands except Ni'ihau and Lana'i, where they have been probably eliminated. They damage drier open ecosystems from low to high elevations. On Maui and Hawai'i, they are found in subalpine woodland and alpine grassland. Goats commonly enter upper elevation wet forest on Maui and in the past also destroyed wet forest remnants on Lana'i. On Moloka'i, Hawai'i, and Maui, goats degrade low elevation dry forest. On Kaua'i, they damage the edge of the Alaka'i Swamp and enter wet habitats in dry periods. Goats have had a major role in the destruction of dryland and mesophytic forest on Ni'ihau and Kaho'olawe in the past (Tomich 1969; Scott et al., in press).

Feral goats are implicated as threats to Haplostachys haplostachya, Abutilon menziesii, Cyanea superba, Hibiscadelphus distans (table 1), and other rare plants (Wagner, Herbst, and Yee, this volume). Effects on koa (Acacia koa) (Spatz and Mueller-Dombois 1973), silver-swords, Haleakala sandalwood (Santalum haleakalae), and other rare trees have been reported (Loope 1982, 1983a; Loope and Scowcroft, this volume). Feral goats had probably eliminated all traces of Canavalia kauensis except the seedbank in the lowlands of Hawai'i Volcanoes National Park. When goats were removed, dormant seeds sprouted, and the plant reappeared (Mueller-Dombois 1981). Goats limit mamane reproduction in Haleakala National Park, and apparently negatively affect reproduction of woody native species such as Canthium odoratum, Dodonaea viscosa, and Osteomeles anthyllidiofolia in Hawai'i Volcanoes National Park (Williams 1980).

Black-tailed and axis deer (Odocoileus hemionus and Axis axis). Blacktails are found on western Kaua'i in dry native and alien forests (Tomich 1969). [Koa and 'ohi'a are native elements of these forests; kukui (Aleurites moluccana) is a Polynesian introduction; and silk oak (Grevillea robusta) and several species of eucalyptus are aliens (Kramer 1971).] Axis deer are found in lowland kiawe, strawberry guava (Psidium cattleianum), and koa haole (Leucaena leucocephala) forests and range into higher 'ohi'a forests on Moloka'i, Lana'i, and Maui (van Riper and van Riper 1982), with a small remnant on O'ahu. Blacktails have threatened rain forest and rare bird habitat in the Alaka'i Swamp in the past. Axis deer and pigs have badly degraded vegetation and soils of East Moloka'i, with attendant damage to coral reefs on the southern coast through siltation (Scott et al., in press). Axis deer are viewed as the most serious existing threat to Lana'i's remaining forest and are a potential threat to mesic and rain forest on Haleakala (Scott et al., in press). Invasion of adjacent rain forest by axis deer may follow creation of open forest by cattle, pigs, or goats.

Feral pigs (Sus scrofa). Feral pigs occur on all major islands except Lana'i and Kaho'olawe (Tomich 1969; van Riper and van Riper 1982). Pigs were apparently present on Laysan Island and Sand Island at Midway Atoll in the late 1800's and early 1900's (Kramer 1971). On Kaua'i, O'ahu and Maui, pigs are restricted to rain forest and grasslands on ranches (Giffin 1978) or in the subalpine forests of Haleakala National Park (Jacobi 1976). According to Giffin (1978) and Kramer (1971), pigs are abundant on Ni'ihau in arid and open areas with kiawe (Zone A of Ripperton and Hosaka 1942). On Hawai'i, pigs are found from coastal drylands through rain forest to the upper slopes of Mauna Loa and Mauna Kea. They have been observed at 3,030 m, according to van Riper and van Riper (1982). In mamane woodlands of Mauna Kea, densities are much lower than in rain forest (Giffin 1978), where pigs apparently reach levels (19-79 /km^2) unmatched elsewhere (Singer 1981).

Feral pigs are the major current modifiers of Hawaiian forests, probably even exceeding damage done by man. Pig damage has reached extreme levels in this century, perhaps as a result of increasing densities as well as expanding distributions. The reasons for this are unclear, although it has been postulated that animal protein in the form of earthworms, and mutualistic relationships with certain dominant alien plants (e.g. Psidium cattleianum, Passiflora mollissima, Myrica faya), have made conditions more favorable for pigs than previously (Diong 1983). Man and pigs together seem to be enhancing pig habitat over time, favoring introduction of alien plants and resulting in accelerating damage in many areas. The role of wild dog control (through poisoning and other means) in recent creation of more favorable pig habitat in some mesic and dry forests is unstudied.

Pigs compound and intensify the problem of alien plant ingress by creating open habitats through digging up, eating, and trampling native species, and by increasing soil fertility. Pig activity thus works against reestablishment of many native plants adapted to poor soils, and favors establishment of alien plants (this will be discussed further in the section entitled "Nutrient Cycling"). Pigs also transport plant propagules in their feces and pelage. The spread of alien weeds since 1945 in Kipahulu Valley seems well correlated with pig range extension (C.W. Smith and L.L. Loope, pers. comm.). Large areas can be affected by pig activity. It has been calculated that feral pigs in the Kilauea Forest Reserve on Hawai'i dig up over half of the diggable area in a year's time (Cooray and Mueller-Dombois 1981).

Alien plants enhanced by pig activity in Hawai'i, in addition to those noted above, include: Ageratina riparia, Rubus penetrans, Hedychium spp., Sonchus spp., Buddleja asiatica, Phaius tankervilliae, Anemone hupehensis, Andropogon spp., Paspalum spp., Setaria palmifolia, Solanum pseudo-capsicum, Psidium guajava, and Passiflora ligularis (J.K. Baker, unpubl. data).

That the exclusion or removal of pigs can result in recovery of native vegetation and changed plant composition has been quantified through exclosure studies in rain forests (Katahira 1980; Higashino and Stone 1982), and in subalpine grasslands (Spatz and Mueller-Dombois 1975; Jacobi 1976). Some native species seem able to remain stable or increase in the absence of pigs over varying periods of time in different areas, but continued disturbance often favors aliens. In subalpine grasslands in Hawai'i Volcanoes and Haleakala National Parks where pig disturbance continued, native Deschampsia australis and Panicum tenuifolium were replaced by Holcus lanataus (Spatz and Mueller-Dombois 1975; Jacobi 1976). Pigs severely damage fragile and limited communities, such as Haleakala greensword (Argyroxiphium virescens) and Oreobolus furcatus and Carex svenonis bogs on Hawai'i, Maui, and Kaua'i (Gagne 1982; Loope 1983a).

Feral pigs selectively take certain native plant species, thereby reducing already limited populations or confining them to high epiphytic strata (e.g. Astelia). Tree ferns (Cibotium spp.) and Sadleria spp. are preferred items, as are other ferns (e.g. Marattia and Pteridium), Astelia spp., Freycinetia, and various Lobeliaceae and Labiatae. Pigs trample Peperomia and break weak stems of native Cyrtandra, mints (Phyllostegia spp. and Stenogyne spp.), and orchids (Loope 1983b) and are specifically identified as a threat to the candidate endangered species Cyanea superba and the listed Vicia menziesii (table 1). Seedlings of dominant plants such as koa, mamane, and pilo (Coprosma spp.) may sometimes be taken in numbers great enough to affect forest composition, growth forms, and succession over large areas (Diong 1983; J.K. Baker, unpubl. data).

Black and Polynesian rats (Rattus rattus and R. exulans). Black (roof or ship) and Polynesian rats are found on all major Hawaiian islands (Tomich 1969; van Riper and van Riper 1982), often in the same vegetation type. Tomich (1969) indicated that black rats are also present on Sand and Eastern Islands at Midway and possibly other islands, whereas Polynesian rats may also inhabit Ni'ihau, Ka'ula (off Ni'ihau), Kure Atoll (at northeastern end of the chain) and some other islands. Although R. exulans characteristically favors lowlands and R. rattus low and mid elevations (Tomich 1969; van Riper and van Riper 1982), both species are adaptable and found at higher elevations, sometimes in substantial numbers. The black rat occurs to 2,970 m around buildings at Haleakala National Park (Tomich 1969) and to at least 2,440 m in Hawai'i Volcanoes National Park (Tomich 1981). The Polynesian rat has been trapped at 2,060 m in Kipahulu Valley on Maui, and both species are common in wet koa and wet 'ohi'a and are present in scrub 'ohi'a vegetation types there (Stone et al. 1984). In Hawai'i Volcanoes National Park, black rats were 3 times as trappable in rain forest as in mesic forest (C.A. Russell and C.P. Stone, unpubl. data).

Black rats damage flowers, fruit, and bark of Hibiscadelphus (Baker and Allen 1976; Russell 1980), and bark of Osmanthus sandwicensis, Acacia koa, Coprosma rhynchocarpa, and Pittosporum spp. Damage to fruit of Pittosporum hosmeri and Santalum paniculatum has also been noted. The importance of rats as depredators and pollinators of Freycinetia (Perkins 1903) has recently been questioned (Cox 1983), but probably prematurely.

Black rats in rain forests at Hawai'i Volcanoes National Park consume green plants and seeds more frequently than adult or immature insects. Plants taken include Fragaria vesca, Rubus rosaefolius, Physalis peruviana, Vaccinium calycinum, and V. reticulatum. Seeds of Carex wahuensis, Microlaena stipoides, Paspalum dilatatum, and Sacciolepis indica were eaten (C.A. Russell and C.P. Stone, unpubl. data).

Black rats in mesic forests at Hawai'i Volcanoes National Park ate green plant material more frequently than insect larvae. Adult insects were taken even less frequently. Seeds dominated in summer diets and green plants in winter (C.A. Russell and C.P. Stone, unpubl.

data). Rat food habits and densities in different vegetation types are being further analyzed for populations in native forests of Kipahulu Valley and Hawai'i Volcanoes National Park.

House Mice (*Mus musculus*). This species has one of the most widespread geographical and ecological distributions of any of the alien mammals in Hawai'i. It is abundant over a wide range of vegetation types on all of the main islands, at Midway Islands, and on many islets. Mice range from sea level to 3,920 m (Tomich 1969; van Riper and van Riper 1982). Data on comparative densities in vegetational zones are not available, but mice are probably most abundant in lowland habitats, and populations are known to sometimes erupt in "drier beach, grassland, scrub, and forest areas," for example on Maui, Hawai'i, and Kaho'olawe (Tomich 1969; R.L. Walker, pers. comm.). On Maui, substantial populations may exist in wet forests over 1,200 m in some areas, but not in others; possible reasons for this are under investigation (Stone et al. 1984). Little information on *Mus* food habits in Hawai'i is available, but in the lowlands, invertebrates, grass seeds, fruit, and other items are taken (Kami 1966). Much more needs to be known about the impacts of this ubiquitous alien on native Hawaiian systems.

Predation

Small Indian mongooses (*Herpestes auropunctatus*). Mongooses are present on all main islands except Kaua'i (possibly), Lana'i, Kaho'olawe, and Ni'ihau (Tomich 1969). The species ranges from sea level to above timberline and is generally most abundant at lower elevations (less than 600 m) on windward coasts. Small to moderate populations occur from 600-1,200 m in mesic vegetation (Baldwin, Schwartz, and Schwartz 1952) and in subalpine vegetation (Banko and Manuwal 1982; C.P. Stone, unpubl. data). However, at favorable locations, a strict elevational gradient may not hold. Limited data from Hawai'i Volcanoes National Park suggest twice as many mongooses in mesic forests at about 1,880 m as in rain forest at 1,160 m and one to several times as many animals at 30 m in coastal grasslands with alien grasses and shrubs as at higher elevations (C.P. Stone, unpubl. data; C.A. Russell and C.P. Stone, unpubl. data).

Mongooses undoubtedly disperse strawberry guava and other alien plants (Baldwin, Schwartz, and Schwartz 1952) and prey upon colonial seabirds (King and Gould 1967; Simons 1983) and marine organisms (LaRivers 1948; Baldwin, Schwartz, and Schwartz 1952), but for purposes of this discussion, predation on native land animals will be emphasized.

Predation upon Hawaiian crow or 'alala (Corvus hawaiiensis) fledglings (Giffin 1983) and nene (Nesochen sandvicensis) eggs and incubating females (Banko 1982) are the most important obvious effects of mongooses on native animals in Hawai'i at present. Predation on nene in subalpine nesting areas where mongooses are often scarce may be less frequent than predation in the lowlands where mongooses are more abundant, but it is still a major mortality factor for geese. However, vegetational cover is also important: mongoose predation on pheasant nests was higher in areas of sparse vegetation at low altitudes than in areas of denser cover at higher altitudes, even though mongoose populations were apparently lower in the lower elevation/ sparse vegetation area (Smith and Woodworth 1951). Re-establishment of lowland breeding nene populations probably depends on mongoose reduction there, although other limiting factors such as nutrition may also be important (Banko 1982; Stone et al. 1983). Mongoose control in relatively undisturbed mesic koa-'ohi'a forest currently used by the 'alala (Burr et al. 1982) seems necessary. The rarity of red junglefowl on many islands has been attributed to cat and mongoose predation to a varying degree (Berger 1981). Effects of mongooses on low nesting forest passerines are unknown.

Baldwin, Schwartz, and Schwartz (1952) considered invertebrates, including Lepidoptera, Orthoptera, Coleoptera, Hymenoptera, Diptera, Isopoda, and Arachnida, to be important in the mongoose diet. That many of the taxa taken are alien, may be more a function of location of collections than an indication of little impact on native invertebrates. More information on effects of this opportunistic carnivore on birds, plants, and invertebrates in Hawai'i's native ecosystems is needed.

Feral cats (Felis catus). Feral cats occur on all main islands and on other islands in the chain. They were common in the forests of some islands by the mid 1800's (Scott et al., in press). Cats are probably most abundant at low and middle elevations, near human habitations, and in drier areas (Tomich 1969; van Riper and van Riper 1982), but they are found wild in remote areas such as Kipahulu Valley rain forests and in mesic forests at high elevations on Mauna Loa (C.P. Stone, unpubl. data).

Cats may have contributed to the extinction of the Hawaiian rail (Porzana sandwichensis) and are presently important predators on sea bird nesting colonies (Berger 1981; Simons 1983; J.L. Sincock, pers. comm.). Adverse effects on native terrestrial birds probably are limited to those that nest on the ground or low in the understory. Red junglefowl may have been extirpated by cats and mongooses on some islands, although other factors were undoubtedly involved (Berger 1981). Effects on nene populations are unknown, but the nocturnal habits of cats might facilitate killing of females on nests as well as goslings. Forest birds that would likely be vulnerable because they forage in the understory include 'elepaio (Chasiempis sandwichensis), Hawaiian thrush or 'oma'o (Phaeornis obscurus), puaiohi (P. palmeri), Maui parrotbill (Pseudonestor xanthophrys), and po'ouli (Melamprosops phaeosoma), according to Scott et al. (in press). Young 'alala, as mentioned earlier, are also vulnerable when on or near the ground. Tomich (1969) reported lepidopteran remains in the tracts of 2 cats collected on Mauna Kea, but it is unlikely that the impact on native invertebrates is great. C. van Riper III (unpubl. data) found birds in 6 of 9 cat stomachs from Mauna Kea (5 with passerines) and rodents and snails in the other 3 stomachs. Cat stomachs and scats collected in native forests should be saved and analyzed so that a data base can be accumulated.

Black and Polynesian rats. The distributions of black and Polynesian rats are given above. Black rats were thought to have caused the extinction of transplanted Laysan rails (Porzanula palmeri) and Laysan finches (Telespyza cantans) at Midway Islands (Tomich 1969); to have been partly responsible for extinction of the Hawaiian rail (Berger 1981); and to adversely affect dark-rumped petrel (Pterodroma phaeopygia) colonies in Haleakala National Park (Simons 1983). Polynesian rats prey on Laysan albatrosses (Diomedea immutabilis) and other seabirds (Kepler 1967; Tomich 1969).

Past impacts of arboreal black rats on native forest birds are assumed to have been enormous (Atkinson 1977). Reductions of forest birds elsewhere in the Pacific followed introduction of black rats, and decreases of such forest birds as Maui parrotbill, 'o'u (Psittirostra psittacea), crested honeycreeper (Palmeria dolei), and 'akiapola'au (Hemignathus munroi) as a result of black rat irruptions in Hawai'i were suggested by Atkinson (1977). Rat predation (probably R. rattus) may have helped reduce populations of the cavity-nesting Kaua'i 'o'o (Moho braccatus), according to Scott et al. (in press). Probably other cavity-nesting species have also been affected. 'Apapane (Himatione sanguinea) feathers were found in one of 86 stomachs from black rats taken in native rain forest on Hawai'i (C.A. Russell and C.P. Stone, unpubl. data).

Black rats were reported to prey on land mollusks by Perkins (1903). In the montane rain forest on Hawai'i, adult insects occurred in 32%, insect larvae in 17%, and annelids in 9% of 86 stomachs collected

(C.A. Russell and C.P. Stone, unpubl. data). Adult and larval insects occurred more frequently in winter, and annelids in summer. Adult insects taken were in the orders Diptera, Hemiptera, and Hymenoptera, while larvae were in the orders Coleoptera and Lepidoptera. Further work on diets of both species of rats in Kipahulu Valley is under way under National Park Service contract with B.P. Bishop Museum (Stone et al. 1984).

Interspecific Competition

Native and alien birds. Banko and Banko (1976) concluded that 3 introduced avian species--the common myna (*Acridotheres tristis*), Japanese white-eye (*Zosterops japonica*), and red-billed leiothrix (*Leiothrix lutea*)--had potential roles in reducing populations of native forest birds, on the basis of habitat overlap and food habits. They traced the introductions and histories of populations of each species in Hawai'i. The barn owl, *Tyto alba*, was not believed to be a serious threat to the 'io, *Buteo solitaris*, or the short-eared owl, *Asio flammeus*, in the past or at present (Banko and Banko, n.d.). Competition for, and reduction of, such important lepidopteran taxa as Geometridae, Pyralidae and other food resources, especially during the nesting season of native birds, is presumed. Banko (1978) and Gagne (1980) also outlined the deleterious effects of continental flies and wasps on insects that were formerly important foods for 'o'u, Hawai'i creeper (*Oreomystis mana*), palila (*Loxioides bailleui*), and 'oma'o, among other species. Competition could have been particularly important at the height of alien bird population expansion (Banko and Banko, n.d.), especially if coupled with a diminished prey base resulting from insect predation, parasitism and diseases. Atkinson (1977), using a similar historical/ecological approach, also concluded that the melodious laughing-thrush or hwa-mei, *Garrulax canorus*, might be a factor in competition with native birds, based on widespread distribution of this species in Hawaiian forests. However, he judged that the introduction was too late to implicate the hwa-mei in major declines of native birds.

Ralph (1978) suggested that among 10 common passerines in Hawai'i Island forests, "interspecific actions appear to play a secondary role at most times." His data have not yet been fully analyzed or published.

Conant (1981) studied distributions and densities of 8 alien and 9 native birds on Mauna Loa and concluded that *Leiothrix* may have displaced the 'oma'o or Hawaiian thrush in mountain parkland, savanna and 'ohi'a dry forest. Although Japanese white-eyes invaded closed rain forest in considerable numbers, competition was thought to be of little importance in controlling distribution of natives. Conant noted, however, that species densities could be limited to the detriment of less aggressive competitors around scarce nectar sources.

Van Riper (1976) hypothesized competition between the common 'amakihi, Hemignathus virens, and Japanese white-eye in 'amakihi territories. He found that although lack of mamane nectar could prevent breeding, excess nectar (provided by him) resulted in increased territorial defense and low breeding success (van Riper 1984). The precise influence of Zosterops was not determined in his study, but it could be crucial depending on food resources and population levels. Conant (1976) provided some evidence that common 'amakihi and 'apapane affect each other's densities depending upon whether or not nectar is the main food resource (if it is, 'apapane densities exceed those of 'amakihi); however, she noted that rainfall and other parameters [perhaps often including competition with Zosterops] may also define optimum habitats for both species.

Pimm and Pimm (1982) suggested that more dominant native species such as the 'i'iwi, Vestiaria coccinea, and several extinct and endangered honeycreepers were less able to subsist on marginal resources than less aggressive competitors such as 'apapane and 'amakihi. Alien species such as Zosterops might adversely affect such dominants by forcing increased territorial defense at good nectar sites (preferred species with many blooms); by relegation to less favorable sites (preferred species with fewer blooms or secondary tree species); or through reducing and further dispersing an already dispersed nectar supply.

Scott et al. (in press) discussed distributions, habitat occurrences, and densities of alien bird species in Hawai'i. Space is not available here to cover possible competitive interactions species by species, but alien bird richness was highest in dry woodlands below 1,500 m with introduced plant understories. It was noted that few introduced gamebirds penetrate closed forests, and that disturbed habitats contain more alien bird species than undisturbed. Disturbed forests allow avenues of ingress for alien birds, according to the authors.

Mountainspring and Scott (in press) used partial correlation matrices for paired species (with habitat effects removed), to infer competition (for food) among alien and native forest passerines. The bulk of significant correlations were positive (67% of total), suggesting species association rather than competitive avoidance. The authors noted that such species as the omnivorous Zosterops, Leiothrix, and Garrulax; the insectivorous 'elepaio, Kaua'i creeper (Oreomystis bairdi), 'akepa (Loxops coccineus), and common 'amakihi; and the nectarivorous 'apapane and 'i'iwi showed positive associations. Increasingly or decreasingly favorable habitat for a particular guild was evidently similarly responded to by all species in the guild across a variety of locations on each island. The only consistent negative partial correlations (presumed to indicate competitive avoidance) were for Zosterops/Chasiempsis on windward Hawai'i and Zosterops/Vestiaria in montane forests on Hawai'i. Scott et al. (in press) hypothesized competition for understory insects to explain the first relationship and competition for lower quality (dispersed?) nectar to explain the second. As noted earlier, increased territorial defense by Vestiaria may be another (not exclusive) explanation for negative associations over the long term.

Native birds and rats. Atkinson (1977) noted that many Hawaiian forest birds depend on nectar or insects for food, but thought that many insects are unavailable to rats because they are too small or impossible for rats to reach. This generalization has not been investigated. Perkins (1903) pointed to the depredation of rats (probably the more arboreal R. rattus) on Freycinetia arborea fruit. Since 'o'u and 'alala also depended heavily on this fruit, rats may have especially competed with them when and where rats and 'o'u and/or 'alala were abundant (Banko and Banko, n.d.).

Based on our knowledge of rat food habits in Hawai'i (see previous discussions) it seems that direct competition would be likely for native birds that specialize on fruit and large conspicuous invertebrates that are active day and night. However, insect eggs, pupae, and many small invertebrates on and above ground level might be vulnerable to both birds and rats. Thrushes and perhaps po'ouli (a specialist on snails, according to Baldwin and Casey 1983) are among native birds that may compete with rats, in addition to species already mentioned. However, almost nothing is known of dynamic interrelationships among rats (both species), plants and invertebrates in thrush and po'ouli habitats. (The same interrelationships should also be studied in similar areas not frequented by those avian species, for comparison.) Information on rats and their adverse effects in other important forest bird habitat is also lacking, but preliminary data on rat densities and food habits and bird abundance from several areas in Kipahulu Valley are being analyzed (Stone et al. 1984).

Habitat Degradation

Optimum habitat for a native animal may be considered as the natural complex of physical and biological factors in which a population is at a peak that can be sustained over time without damage to the habitat (carrying capacity). Introduction of most alien elements usually degrades the optimum habitat for native species. Alien diseases, predators, and competitors of vertebrates have already been discussed, or will be discussed elsewhere (van Riper and van Riper, this volume). Additional man-influenced changes such as grazing, clearing land for agriculture, burning, and lumbering (cow, plow, fire, and ax) also destroy or degrade habitat for many natives, but these effects are not the subject of this paper. Direct effects of alien animal depredations on native plants and ecosystems were discussed above, but not in the context of native animal habitat. This will be touched on here, largely in relation to native birds (Gagne and Christensen, this volume, address invertebrate habitat). Information is largely taken from Banko and Banko (n.d.), and the large volume of data collected by Scott et al. (in press) during the U.S. Fish and Wildlife Service Hawai'i Forest Bird Survey.

Effects of feral sheep and goats on nene habitat were judged important in local population impacts by Baldwin (1947). Cattle, goats, and possibly pigs were believed highly important factors in nene habitat degradation in the mid-1850's and later (Banko and Banko, n.d.). Effects begun then, together with invasion of alien plants, may have permanently altered considerable habitat.

Grazing by sheep and cattle was partly responsible for eliminating, fragmenting, and degrading high-elevation akiapola'au habitat (Scott et al., in press). Effects of feral sheep, goats, and mouflon on mamane habitat of the Federally endangered palila were serious enough to force a court order to remove the feral sheep and goats from Mauna Kea (Kobayashi 1979; Scowcroft 1983). Cattle grazing and lumber harvest on leeward Hawai'i severely affected habitat of 'akepa, Hawai'i creeper, and 'alala. According to Giffin, Scott, and Mountainspring (in prep.), nearly all of the undisturbed and none of the disturbed koa-'ohi'a forests in Kona were once occupied by crows. However, P.C. Banko (pers. comm.) has found breeding 'alala in koa-'ohi'a forests that were highly disturbed by cattle and other activities. Scott et al. (in press) said that cattle damage to forest understories on their Kohala study area on Hawai'i correlated with low densities of 'elepaio.

Feral ungulates were thought responsible for the lower 'amakihi densities in Maui dry forests than in similar dry forest habitat on Hawai'i. On Moloka'i, 'apapane are absent or present in low densities as a result of deforestation by axis deer, pigs, goats and cattle. On East Moloka'i, loss of 'amakihi is tied to axis deer depredations.

Feral pigs are important in the reduction of certain Hawaiian lobeliads, especially in wet forests (Diong 1983). Native birds that use these taxa include Bishop's 'o'o, Moho bishopi (if extant); the 'i'iwi; and the 'o'u (Scott et al., in press). Bishop's 'o'o may be especially sensitive to habitat degradation caused by pigs, partly because of lobeliad reduction. Pigs (and rats) also consume Freycinetia, favored by 'o'u and 'alala, and probably lower habitat quality of these birds accordingly.

Feral pigs may have negative effects on the Federally endangered Pseudonestor and Melamprosops. Both favor dense forest understories for foraging, and feral pigs are effective in simplifying understory composition and structure. Casey, Mountainspring and Scott (in prep.) showed that po'ouli habitat had "light pig damage and well developed herb, ground fern, and moss layers." They hypothesized destruction by pigs of microhabitat needed for land snails and other invertebrates favored by po'ouli.

Habitat degradation by feral pigs is also thought to affect Hawai'i creeper, 'akepa, and 'elepaio on Hawai'i; and Kaua'i thrush, small Kaua'i thrush, and the Kaua'i 'o'o on Kaua'i. Foraging of crested honeycreepers on Maui on understory nectar producers such as Rubus hawaiiensis when Metrosideros polymorpha blooms are scarce, may also be reduced by feral pig activity (Scott et al., in press).

The role of alien birds in degradation of habitat of native birds may be important. Peak populations of birds that invade forest ecosystems might affect foods (insects and plants) severely enough to permanently reduce habitat quality for natives. Such species as the Japanese white-eye, red-billed leiothrix, and common myna may have already reduced habitat quality by this means in many areas.

Indirect Effects

Impacts on other aliens. The important, and sometimes mutualistic, role of feral pigs in dispersing and encouraging weedy alien plants has been discussed previously. Mongooses, rats, and mice are also responsible for spreading alien plants, but the effects are less obvious and the magnitude uncertain. Alien birds disperse or are closely associated with numerous alien plants, of which Passiflora, Myrica, Schinus, Lantana, and Clidemia are probably the most important in native systems. Warshauer et al. (1983), Lewin (1971), and

Scott et al. (in press) noted associations of the following introduced birds with Passiflora: black francolin (Francolinus francolinus), Erckel's francolin (F. erckelii), gray francolin (F. pondicerianus), kalij pheasant (Lophura leucomelana), common peafowl (Pavo cristatus), wild turkey (Meleagris gallopavo), Leiothrix lutea, mockingbird (Mimus polyglottos), Japanese white-eye, northern cardinal (Cardinalis cardinalis), house finch (Carpodacus mexicanus), and spotted dove (Streptopelia chinensis). Fortunately, many of these species do not penetrate intact forest, but most will use forest openings created by man or feral animals for ingress.

A number of avian species in addition to those mentioned above are associated with alien grasses, herbs or shrubs (Scott et al., in press). They include California quail (Callipeopla californica), ring-necked pheasant (Phasianus colchicus), zebra dove (Geopelia striata), Eurasian skylark (Alauda arvensis) (a good indicator of degraded, fragmented forests), melodious laughing thrush, and nutmeg mannikin (Lonchura punctulata). Overall alien species diversity is highest in broken woodland and is heavily influenced by game bird occurrence. Cardinalis distributes Psidium spp. and Schinus terebinthifolius in lowland forests (Scott et al., in press). In a more subtle relationship among aliens, van Riper (1980) noted that alien birds might be contributing to the spread of naio (Myoporum sandwicense) on Mauna Kea through dispersal of seeds while feral sheep reduce competition from mamane through browsing.

Areas disturbed by feral ungulates contain a greater variety of alien bird species than undisturbed areas (Scott et al., in press). Stock pond and other water sources created by or for cattle are sought out by various game birds, house finches and common mynas, among others. Cattle and pig wallows also attract alien insect vectors of malaria or pox (van Riper and van Riper, this volume) that may thus reduce native bird populations. In some instances, continued presence of ungulates can perpetuate alien plants that would eventually give way to natives in their absence (Loope and Scowcroft, this volume). The establishment of alien plants after disturbance by feral animals, which are then able to maintain permanent populations in the absence of animals through allelopathy, monotypic stands, or altered nutrient cycles, has also been noted (Smith, this volume). The encouragement of introduced vegetation via alien animal distribution and cultivation contributes an alien fauna of snails, insects, spiders, other invertebrates, and plant pathogens (Howarth, this volume). Ecosystem modifications caused by the negative effects of these associated aliens on native vertebrates and invertebrates could be tremendous.

Forest openings do not always need to be caused by man or his associates to encourage alien birds. The apparently natural phenomenon in Hawaiian forests called 'ohi'a dieback (Mueller-Dombois, this volume) is correlated with reduced native and increased introduced birds. In scattered dieback sites in the Hamakua area of Hawai'i, 'apapane, 'i'iwi, 'oma'o, and 'elepaio numbers were 70, 77, 47, and 93% lower than in tall, closed canopy forest. Red-billed leiothrix and Japanese white-eye numbers were 30 and 34% higher (Scott et al., in press). Patchiness of vegetation of different sorts can favor native and non-native alike. For example, 'i'iwi and melodious laughing thrush both occur in greater numbers where understory diversity is high; native tree falls may help create such diversity (Scott et al., in press).

Nutrient cycling. Smith (this volume) stated that the effects of alien plants on nutrients in Hawaiian ecosystems deserve special consideration. The danger that aliens such as *Myrica* can, through nitrogen fixation, create their own favorable environment on Hawai'i's young and nitrogen-poor soils was emphasized. A study to determine the role of *Myrica faya* in altering primary succession in Hawai'i Volcanoes National Park has been proposed and funded (P.M. Vitousek, pers. comm.).

Feral pigs also play an important role in altering nutrient cycling in Hawaiian systems. They are distributors of *Myrica faya*, the berries of which average 12% of the total volume of food taken in the Puhimau Unit of Hawai'i Volcanoes National Park (n = 54 adults taken by hunting) on a year-long basis (C.P. Stone, unpubl. data). But probably more importantly, pigs in nitrogen-limited areas can also modify nutrient sinks, availability, and dynamics through their rooting activities. Where pigs are absent, organic material (and nutrients) build up (Higashino and Stone 1982) and ultimately affect soil formation. Where pigs root, the availability of "nitrogen [and other nutrients] to plants and the potential for nitrogen losses to the site (in leaching or denitrification) is greatly increased" (P.M. Vitousek, pers. comm.; Vitousek et al. 1979; Vitousek et al. 1981). Short-term nitrogen availability (favoring alien plant establishment) and long-term nitrogen loss (preventing the usual succession of natives) may be the pattern on such sites, especially if pig disturbance continues. Parent soil materials (ash, pahoehoe, or 'a'a) also affect nutrients, and the long-term advantages of nitrogen-fixers on some sites may not always hold as nutrient availability changes (Vitousek, Van Cleve, and Balakrishnan, in press). However, the continual influx of alien plant species is likely on pig-altered sites. The effects on plant and animal succession and community composition as a result of altered nutrient availability alone could be substantial. Pigs also alter ecosystem structure and processes through trampling, alien propagule introduction and enhancement, reproductive reduction of natives, and soil erosion, as noted above. Pig rooting and defecation favor alien soil invertebrates, further altering nutrient cycling (Howarth, this volume).

REDUCTION OF ALIEN IMPACTS

It should go without saying that extreme care must be exercised in the introduction and translocation of alien birds and mammals in Hawai'i. The best way to manage aliens is to prevent new species from entering the State and to prevent aliens that are present from affecting additional areas. As indicated in table 2, introductions that have recently succeeded are occurring at a much more rapid rate than introductions by either Polynesians or nature prior to man. The Hawai'i Department of Agriculture (DOA) and the Department of Land and Natural Resources (DLNR) have responsibility for controlling the introduction of vertebrates under Chapter 150A, Part II of Hawai'i Revised Statutes (HRS) and Chapter 187, Sect 1.2, HRS (Burr 1984). DOA administers Chapter 150A and maintains a list of prohibited entry species. It is expected to confiscate animals and charge the owners for expenses. DLNR administers Chapter 187, which covers translocation from one area in the State to another as well as importation. However, only the introductions proposed by DLNR are covered; other proposals are not addressed. If an animal escapes, it is classified as "wild" and a permit is required under Chapter 191 to control or eliminate it when it is involved in agricultural damage, is a nuisance, or is a health hazard (Burr 1984). The DLNR and DOA cooperate closely on updating the DOA list of restricted or prohibited entry species. There have been recommendations to develop a list of species that should be exempted from the wild bird protection provision.

Complexities of Damage Control

"Ecology may not only be more complex than we think; it may be more complex than we can think" (F. Egler). Perhaps the major problem in understanding the true impacts of aliens and devising management strategies to reduce them is the number of confounded parameters involved. Before damage can be understood, predicted, and overcome, one may need to know how interactions occur among: soil fertility, weather, land use

Table 2. Successful colonizations of mammals and birds in Hawaii during different time periods.

	Native Species (20 million yrs)	Polynesian Introductions (1500 years)	Historical Introductions (200 years)
Land Mammals	1	3	18
Years per Successful Species	20,000,000	500	11
Land Birds	20*	1	45
Years per Successful Species	1,000,000	1500	4

* These underwent considerable adaptive radiation to form 35 extant species and many now extinct species (see Olson and James 1982).

history, plant phenology, predation, competition and other interrelationships with many species; population structure, density, distribution, and dynamics; animal movements, nutrition, and the vegetation complex. Such knowledge does not come cheaply or in a short time or from one study area, because problem vertebrates are long-lived, mobile, adaptable, and difficult to observe. Good information on one parameter, such as population density, may be misleading (Van Horne 1983). For example, high densities of young animals might be indicative of poor habitat, which is occupied by young because of social dominance by adults elsewhere, or because of high reproductive success and temporary survival. Attempting to reduce vulnerable problem animals in such situations might not be efficacious.

Other information required for good control programs includes the effects of different population levels upon the resource at risk, the cost of conducting the control, the value of the resource protected, effects of control on nontarget animals, effects of control on the resources being protected and on the ecosystem, the amount and length of followup needed, and feedback as to the effect on the problem animals. Managers need to establish long- and short-term priorities to determine what resources can be brought to bear on problem animals in different ecosystems and situations. To predict effectiveness of control under established time and budget constraints, animal populations and productivity should be compared (through responsive models) to determine the optimum efforts to achieve the desired reduction in damage. Proper monitoring of control effects necessitates systematic sampling of both animal populations and the resources that they damage. This should really be done pre and post control at a minimum.

The goal of reducing the effects of introduced vertebrates upon Hawaiian ecosystems is not accepted by everyone. Some believe that nothing can be done; others that it is too expensive and/or time consuming; and others consider that alien vertebrates add scientific, aesthetic, social, recreational, or even cultural and religious values that are more important than the values of native ecosystems. Studies of the importance of these values in the minds of Hawai'i's citizens, and of the economics involved, have not yet been made; however, most informed people (probably a distressingly small portion of any population!) would probably agree that preservation and management of native ecosystems in some areas is necessary and desirable. There is now overwhelming evidence that in Hawai'i this depends upon reduction or elimination of alien vertebrate impacts. To eliminate the adverse effects, it is necessary to consider killing or excluding the aliens, at least "temporarily." The fact that individual animals can't just be killed "temporarily" raises a conflict about the value of life. So a decision to reduce the adverse effects of alien vertebrates becomes a complicated economic, social, political, ethical, aesthetic, recreational, scientific, and land use decision. It also involves a worldwide, as well as a local, community of interest in Hawaiian ecosystems. Let's assume we have somehow made the decision to control alien vertebrates to benefit native Hawaiian ecosystems in some areas. Then what?

Depredations

"Good fences make good neighbors" (R. Frost). If opposing land uses such as sustained yield recreational hunting and native ecosystem preservation and management are to be supported and perpetuated (and this seems realistic), feral ungulates must be excluded from some areas and perpetuated in others. Fence construction is costly and maintenance is continual, but there is no other way to sustain adjacent land uses with these opposing objectives. Programs in Hawai'i Volcanoes and Haleakala National Parks to reduce and eventually eliminate feral goats and pigs are examples of ungulate control programs that depend upon fences. The question of who should build and maintain fences deserves further discussion elsewhere, but in this case the Federal government is assuming the sole responsibility for perpetuating Hawai'i's native ecosystems.

Once fences are constructed, reduction of the animals by hunting, snaring, trapping, or poisoning is possible. Removal of live animals for use elsewhere is usually expensive and time consuming, requires a place to put the animals, generally costs more than it is worth biologically, and does not usually result in elimination of the all-important last animals that can quickly repopulate the area with offspring. There are, of course, political and social considerations. Drift fences may be used to restrict animal movements within fenced areas or to direct animals toward accessible areas for removal. Internal barriers consisting of combinations of fences and topographic features may be necessary to delimit areas from which animals can be effectively removed. Such areas should be large enough to reduce major fencing costs and avoid artificial paddock-like situations, but small enough to allow efficient elimination of animals with the resources available.

Public hunting may be used as a tool to reduce depredations of ungulates in some instances, but management by public hunting alone usually results in sustained yield. Hunting as a control method is most effective where habitat is limited and accessible. Removal of sheep from Mauna Kea and goats and pigs from parts of Hawai'i Volcanoes National Park has taken an organized, sustained use of agency "shooters" in conjunction with public "hunters." Barrett and Stone (1983) found that the Deputy Ranger or Citizen Hunter Program active in Hawai'i Volcanoes since 1972 was not effective in reducing feral pig populations except in highly accessible areas (within 500 m of a road). The average removal rate by citizen hunters (percentage of estimated carrying capacity) was 3% of the adult pig population every 6 months; 30-40% should be removed if populations are to be reduced to extinction in a 3-5 year period. Through use of agency hunters and dogs, we have achieved an estimated removal rate (as of May 1984) of 25% in one rain forest unit and over 50% in a mesic forest (Stone and Taylor 1984).

The Hawai'i Department of Land and Natural Resources recognized the need to manage ungulates within native ecosystems in the Hawai'i Wildlife Plan (Hawai'i Division of Forestry and Wildlife 1983:63):

> Where the presence of big game populations within sensitive native ecosystems is destructive, elimination can be accomplished through public or staff hunting opportunities.... Where the public hunting is inadequate in removing excess game animals, drives and trapping should be employed, but only as a last resort due to the high costs.... Feral pig, goat and sheep populations should be monitored and maintained at levels resulting in minimum damage to watersheds and native ecosystem protection and should be controlled by public hunting whenever possible.... In Natural Area Reserves, the objective should be to reduce feral game mammals to the lowest possible levels using public hunting.

When combined with fencing and critical evaluation, and if organized properly, such programs might keep some populations in check. However, in most valuable natural areas, the goal should be elimination of ungulates rather than sustained yield, even at low population levels. The potential for increase when even a few animals remain is large.

Control of depredating ungulates with chemical toxicants is a controversial and expensive proposition, but it deserves further consideration in Hawai'i, considering the magnitude of the problem and the scarcity of secondary and non-target animals. No toxicants are currently registered for use with ungulates. Chemical use entails a complicated process of registration, classification, labeling, and certification under the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA) of 1974 and the Federal Environmental Pesticide Control Act of 1972, administered by the Environmental Protection Agency (EPA) (Hood 1978). Use of toxicants for pig control in remote areas in Hawai'i would probably necessitate registration under Section 24 of FIFRA, which provides that a state may register pesticides formulated for distribution and use within that state to meet special local needs, if the state is certified by EPA as capable of administering the Act. Alternative emergency provisions under Section 18 of FIFRA, or Experimental Use Permits (EUP) for chemical use also exist under more limited conditions of research and/or area of application.

The use of chemicals is neither a panacea nor an environmental disaster. Chemicals can be used safely and effectively in some cases and can have certain advantages such as low cost (once registered), target species specificity, non-specificity within a population (all sexes and ages are vulnerable), and ease of use in remote areas. However, chemical effectiveness usually depends upon bait acceptance, and some animals may be difficult to attract to bait--e.g. feral pigs (J. Hone, pers. comm.; R.H. Barrett, pers. comm.; C.P. Stone, unpubl. data). Chemicals, like other animal control tools, must be repeatedly used as long as reproducing animals remain. Complete reliance on chemicals, biocontrol, fences, hunting, or any one tool is unrealistic, but all appropriate control methods should be developed and improved for use where needed. Although registering a toxicant is costly, information gathered in responsible research/management programs will be useful in meeting eventual registration requirements. Toxicants will likely be needed to control some species in some situations (see discussion below).

A number of research/management emphases are essential in well-conducted depredation control programs, and considerable research information and continual feedback are usually necessary. Some idea of ungulate population size, sex, and age structure, reproductive rate, and distribution in the control unit is necessary to determine whether rate of removal is sufficient to effect reduction. Information on rate of removal should be continually recorded and compared with theoretical or known reproduction and mortality. Indexes to the population being removed and to the resources being damaged are required to determine progress and adjust control strategies. Supplemental information on animal movements through radio telemetry is useful in improving and adjusting control strategies to changing animal behavior and densities. Data on food habits may also provide cues to vulnerability or shifting behavior patterns as control progresses.

Primary emphases in ungulate control programs should be:

1. The necessity for efforts lasting many years.
2. Continual learning and feedback about success of control (monitoring).
3. Provision for sufficient resources to effect reduction.
4. The development of multiple methods to reduce animals.

It is likely that what will work in one area at one population level will not be as useful under different conditions. To summarize alliteratively, multiples [years and methods], money, monitoring, and modification are keys to controlling depredations by ungulates in Hawai'i.

Predation

"Well, so much for the unicorns" [said Noah, standing over 2 carcasses]. "From now on all carnivores will be confined to C deck" ("The Far Side"). Some things just don't mix, and the best way to preserve one is to get rid of the other. It is generally true that when predators need to be "controlled" to preserve and manage native Hawaiian ecosystems, the best way is to kill them. Mongooses, cats, and rats simply cannot be effectively excluded or repelled or trapped and transplanted in most situations in the wild. Again, this is a controversial matter with many ramifications beyond the ecological, but let's assume we have opted for controlling predator impacts.

Predator damage may sometimes be controlled by trapping where the plant or animal to be protected is restricted in distribution. Examples are protection of dark-rumped petrels from mongooses, cats, and rats at breeding colonies (Simons 1983); protection of nene in release pens in backcountry situations (N. Santos, pers. comm.; H. Hoshide, pers. comm.); removal of mongooses around an 'alala nest (Giffin 1983); or protection of a group of rare trees from rats (C. Zimmer, pers. comm.). Shooting and trapping have been effective in removing cats from somewhat limited areas (e.g. 415 ha Jarvis Island) (Rauzon 1983), if enough manpower is available. However, chemical toxicants are necessary in most cases where the resource to be protected from predators is dispersed over a large area or over time.

Several rodenticides have been registered for agricultural use and some laboratory and field work has been done on mongoose and cat toxicants (Woodworth and Woodside 1953; Kridler 1966; L. Pank, pers. comm.). Risk to other animals (nontarget hazards) and to animals that eat poisoned animals (secondary hazards) are minimal in Hawai'i, at least insofar as native species are concerned. Nevertheless, we need quantitative information about these hazards; about baiting techniques in native ecosystems (including bait spacing, timing, substrate, and doses); more lab research on toxicity levels, acceptance, and appropriate chemicals; and more information on predator ecology and potential for control in Hawai'i's ecosystems. Basic practical questions of feasibility in terms of reinvasion rates and sizes of areas that can be effectively treated in different situations are largely unaddressed.

A 3-year program headed by the U.S. Fish and Wildlife Service (FWS), with the National Park Service (NPS), and the Hawai'i Division of Forestry and Wildlife (DOFAW) cooperating, has been designed to develop a "drop-bait" toxicant to eliminate or reduce mongooses seasonally in nene and 'alala breeding areas, waterbird habitat, colonial nesting sites for seabirds, and perhaps native forest other than that used by crows. The objective is to obtain a special local need registration under Section 24 of FIFRA (J. Keith, pers. comm.). Current research on rat ecology and control in native forests is under way, with limited efforts in Haleakala and Hawai'i Volcanoes National Parks (Stone et al. 1984; C. Stone, unpubl. data). Funding for a more substantial program of rat and mongoose research may be available from NPS and could be coordinated with the mongoose project headed by FWS. The policy of the DLNR on small alien mammals as stated in the Hawai'i Wildlife Plan is to support research by others on predators and rodents; to implement control only when it is needed and will be effective; and to control only where cost/benefit ratios are favorable (Hawai'i Division of Forestry and Wildlife 1983).

Interspecific Competition

"New questions arise when many populations and entire biomes are being fragmented and reduced on such a scale and at such rates. These questions are a great challenge to the ingenuity of biologists .... Unless we solve them, we will end up with less than we intend, struggling in our ignorance to protect genetically eroding populations and decaying ecosystems" (T. Lovejoy). Despite a number of introductions of alien birds into Hawai'i in the last century (Moulton and Pimm 1983) and documented increases and extinctions of the species and populations involved (Banko and Banko, n.d.), we do not have good quantitative and qualitative information about adverse impacts of introduced birds on the native avifauna. Banko and Banko (n.d.) used an historical/ecological approach to infer competition among different species and in different areas. If food habits of species pairs were similar and alien increases coincided in time with native decreases, competition was assumed to have played a role. Mountainspring and Scott (in press) and Conant (1981) examined densities of various species in different ecosystems at one point in time. Relationships between species pairs that were negative were assumed indicative of competition, and those that were positive, of association, for the purpose of using a common food base or other mutual resource. Variation in relationships with time of year or over a period of years was not considered.

Although both approaches have value, a full understanding of interspecific competition among native and introduced birds in Hawai'i awaits further study. Dynamic relationships throughout the year over a period of years need to be explored. Densities, reproductive rates, mortalities, and movements of potential competitors should be studied in relation to habitat variation (e.g. bloom or insect abundance, rainfall, temperature, population levels of other avian species, impacts of alien mammals, diseases, and other biota) over time. The effects on forest resources (especially during peak alien population levels) need to be determined and the permanence ascertained. Activity budgets, densities, food habits, and reproductive success of native birds in habitats with and without alien birds should be determined.

The potential for additional species of introduced birds to compete with native species still exists. Williams (1983a, b) suggested that red-vented bulbuls (Pycnonotus cafer) may have been deliberately released on O'ahu and on Hawai'i in 1966 and 1982, respectively. The red-whiskered bulbul (P. jacosus) was apparently accidentally released on O'ahu in about 1965. Neither species is noted for colonizing across open water, but both seem to be increasing on O'ahu and may disperse to neighbor islands (Williams 1983b; Conant 1983). Bulbuls are known to be rapid colonizers, agricultural pests, and potential threats to native forest birds. The possibility that these species and other introductions will further reduce forest invertebrates and plants must be taken seriously; initial populations should be removed where possible or closely monitored where not possible.

An important species such as the Japanese white-eye or an irrupting species that cannot be controlled should be followed through introduction or buildup, population irruption, and population decline in several areas, and its impacts on forest resources, including native avian species, should be determined. Japanese white-eyes are currently widespread in native forests but may be declining or on the verge of doing so in some areas already (Dunmire, 1962). The possible increase of the Japanese white-eye and melodious laughing thrush in Kipahulu Valley (Scott et al., in press); the possible expansion of the laughing thrush at lower elevations in Ka'u and Kona; the decline of Leiothrix at low elevations especially on O'ahu (Shallenberger 1981); the close association of Leiothrix and the laughing thrush with increasing naio (van Riper 1980) on Mauna Kea; and the increase of Leiothrix on northwest Haleakala in Kula, are some areas of interest. We need a better understanding of the dynamics of alien bird populations in Hawai'i's forests. More information on rat population dynamics and behavior in different vegetation types, areas, seasons, and years is also needed, to better understand the importance of rats as competitors with the native avifauna.

In addition to better understanding the phenomenon of competition, we need to give further emphasis to the importance of large, intact areas in preserve design. As indicated by Scott et al. (in press), native birds need large undisturbed tracts of native forest to provide buffers against irruptions of alien birds and the perturbations caused by alien birds and mammals. Native invertebrates are also well served by intact native forests (Gagne and Christensen, this volume). Many introduced species in the past, and likely in the future, will be stopped near the forest edges unless there are roads, clearings, or trails into native forests. Activities (including feral animal control) that open and fragment forests, thus enhancing further invasion of alien birds, invertebrates, and plants, need to be carefully evaluated. Optimum sizes of "alien resistant" tracts in different vegetation types should be determined. Vertebrates such as the melodious laughing thrush, Leiothrix, and Zosterops that do presently penetrate largely unmodified forests can have potentially devastating effects on native plant, invertebrate, and avian forms, at least during peak population phases.

Management-Research Coordination

"#!%?$ Ivory tower research!" "#!%?$ seat-of-the-pants management!" (Subdued conversation between a natural resource manager and a researcher). In practice we often take shortcuts in solving problems in natural resource conservation. We don't have enough information, but we must begin to "do something." In acting prematurely we risk making mistakes, but often the problems are severe and call for immediate attention. Waiting for more facts isn't good enough, especially when they accumulate slowly. It is important that if we are to manage without many of the facts needed, however, that we proceed cautiously and learn from our mistakes. Trial and error management of alien vertebrates must be designed to collect data on as many aspects of the ecology of damage as possible. Management efforts should be treated as experiments with replicates, controls, proper experimental design, statistical testing, and reporting (McNab 1983). Research personnel should be directly involved in coordinating with Management to increase the usable information from such "experiments." We cannot afford to further upset Hawai'i's badly disturbed native systems through improper and unguided management experiments. Nor can we afford to waste time in reinventing ineffective strategies and not taking advantage of the knowledge gained through considerable effort elsewhere. Continual and widespread communication of research and management findings is mandatory.

Multiple Approaches and Persistence

"There is no free lunch" (B. Commoner). This is especially true for those of us in Hawai'i who are concerned about managing disturbed and deteriorating ecosystems. History reveals no panaceas for reducing alien animal populations and impacts. Biocontrol, chemical toxicants, hunting, fences, and habitat improvement (for natives) are all useful tools, but all have characteristic disadvantages and varying degrees of impermanence (e.g. Howarth 1983). We need to know more about the entire arsenal of management tools, because different approaches are likely to be effective under different conditions. For example, we are changing feral goat and pig control methods in Hawai'i Volcanoes National Park as population distribution and densities and animal movements and wariness change. The ecological complexities touched upon above make the use of varied combinations of damage reduction methods necessary if management is to be effective. The current approach to damage control, called Integrated Pest Management (IPM), while more generally applied to invertebrates, recognizes that flexible approaches and multiple methods are usually needed to solve agricultural problems far less complicated than those we face in Hawaiian ecosystems (Huffaker 1975; Wilson and Huffaker 1976; Flint and van den Bosch 1981; Ruggiero and Johnston 1984).

Control efforts must be coordinated at research, management, and administrative levels. Realistic long-term goals must be set and receive continued support to attain objectives. Planning and prioritizing for the future by research, management and administration must be carefully done on the basis of facts at hand, and should allow for the continued accumulation of better information and adjusting priorities as we learn. Long-term planning and persistent coordinated efforts and support are essential if we are to reduce adverse effects of alien animals on Hawaiian ecosystems.

TOWARD COOPERATIVE EFFORTS

"If you're not part of the solution, you're part of the problem" (Eldridge Cleaver/Bobby Seale). "We have met the enemy, and he is us" (Pogo). The problem of preserving and managing the remaining examples of Hawai'i's native ecosystems, especially through reduction and elimination of alien vertebrates, goes beyond what any one landowner, manager, or other special interest group (including conservationists) can accomplish. A local and international network of conservationists, developers or consumptive users, land use specialists, natural scientists, businessmen, educators, politicians, sociologists, economists, and other experts must be brought into the process of relating native ecosystems to community, national, and global concerns. The Nature Conservancy of Hawai'i has made considerable progress in this direction, although the initial focus was preservation and management of native bird habitat (a valid indicator for an initial action program), and the areas protected by The Conservancy are small and few, with budgets and staff to match (Holt and Fox, this volume). The State Natural Area Reserves System, now about 20 sites (P.Q. Tomich, pers. comm.), is also appropriate, but again, areas are small and few, and active on-site management is needed.

If the problem of alien animals in Hawai'i's exemplary ecosystems is to be dealt with effectively, a cooperative approach should be implemented. We will need to cooperatively choose important and representative ecosystems upon which to concentrate limited cooperative resources. Our choices should be based on considerations of preserve design, protection, and management. We will need to decide which systems are most intact, most in need of preservation, and least likely to be influenced by aliens and other threats in the future. Increased communication among conservationists and developers would help both groups to better plan for the future. Zones of cooperation and buffer zones around protected areas should be seriously considered in planning (Gregg 1984). We will need to apply intensive, sustained, interdisciplinary research to protected and used areas alike, to understand the ecosystems we are dealing with in biological, socioeconomic, and other contexts. The ecology of aliens in systems managed for multiple use or sustained yield hunting deserves further study in this regard. We will need to know the consequences of periodic irruptions and declines of alien animals and the population biology of natives in protected and unprotected areas, and what governs the dynamics. We will need to fully understand the effects of our management actions on alien animals and on Hawai'i's ecosystems. We will need to explain the rationale and impacts of alien control programs to a wide variety of interested parties for a long time, and invite them to participate in decisions that affect them. We will have to seek a role in decisions made by others that impinge upon our responsiblity of managing protected areas through control of aliens to prevent degredation of ecosystems.

The tasks are enormously complicated, enduring, and time-consuming. Our knowledge of how to proceed, our progress in doing so, and even our communications about the problems involved (except within scientific/ management circles), are rudimentary. But progress is being made, and the end result, reducing the impacts of aliens in Hawai'i's irreplaceable ecosystems, is well worth the effort.

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LITERATURE CITED

Atkinson, I.A.E. 1977. A reassessment of factors, particularly _Rattus rattus_ L., that influenced the decline of endemic forest birds in the Hawaiian Islands. _Pac. Sci._ 31(2):109-133.

Baker, J.K., and S. Allen. 1976. Studies on the endemic Hawaiian genus _Hibiscadelphus_ (hau-kuahiwi). _Proc. 1st Hawaii Volcanoes Natl. Park Nat. Sci. Conf._, 19-22. Honolulu: Univ. Hawaii.

Baldwin, P.H. 1947. Foods of the Hawaiian goose. _Condor_ 49(3):108-120.

Baldwin, P.H., and T.L.C. Casey. 1983. A preliminary list of foods of the poouli. _Elepaio_ 43(7):53-56.

Baldwin, P.H., and G.O. Fagerlund. 1943. The effect of cattle grazing on koa reproduction in Hawaii National Park. _Ecology_ 24(1):118-122.

Baldwin, P.H., C.W. Schwartz, and E.R. Schwartz. 1952. Life history and economic status of the mongoose in Hawaii. _J. Mammal._ 33(3):335-356.

Banko, P.C. 1982. Productivity of wild and captive nene populations. _Proc. 4th Hawaii Volcanoes Natl. Park Nat. Sci. Conf._, 12-32. Honolulu: Univ. Hawaii.

Banko, P.C., and D.A. Manuwal. 1982. _Life history, ecology, and management of nene (Branta sandvicensis) in Hawaii Volcanoes and Haleakala National Parks_. Final Rep., Natl. Park Serv. Contract CX-8000-8-0005. Seattle: Univ. Wash. Coop. Natl. Park Resour. Stud. Unit.

Banko, W.E. 1978. Some limiting factors and research needs of endangered Hawaiian forest birds. _Proc. 2nd Hawaii Volcanoes Natl. Park Nat. Sci. Conf._, 17-25. Honolulu: Univ. Hawaii.

Banko, W.E., and P.C. Banko. 1976. Role of food depletion by foreign organisms in historical decline of Hawaiian forest birds. _Proc. 1st Hawaii Volcanoes Natl. Park Nat. Sci. Conf._, 29-34. Honolulu: Univ. Hawaii.

Banko, W.E., and P.C. Banko. n.d. Decline and extinction of endemic Hawaiian avifauna: role of food depletion and competition by foreign organisms. U.S. Fish Wildl. Serv., Hawaii Volcanoes Natl. Park. Typescript.

Barrett, R.H., III, and C.P. Stone. 1983. Hunting as a control method for wild pigs in Hawaii Volcanoes National Park: a report for Resource Management [Division]. Hawaii Volcanoes Natl. Park. Typescript.

Berger, A.J. 1974. History of exotic birds in Hawaii: first of two installments. Elepaio 35(6):60-65.

Berger, A.J. 1975. History of exotic birds in Hawaii: second and final installment. Elepaio 35(7): 72-80.

Berger, A.J. 1981. Hawaiian birdlife. 2nd ed. Honolulu: Univ. Pr. Hawaii.

Burr, T.A. 1984. Introduced birds in Hawaii and some associated State management problems. Trans. 24th Ann. Hawaii For. Wildl. Conf., 92-97. Honolulu.

Burr, T., P.Q. Tomich, E. Kosaka, W. Kramer, J.M. Scott, E. Kridler, J. Giffin, D. Woodside, and R. Bachman. 1982. Alala recovery plan. U.S. Fish Wildl. Serv., Portland, Ore.

Casey, T.L.C., S. Mountainspring, and J.M. Scott. In prep. Behavioral ecology and limiting factors of the poouli. U.S. Fish Wildl. Serv.

Conant, S. 1976. Bird distribution and abundance above 3000 feet in Hawaii Volcanoes National Park. Proc. 1st Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 63-74. Honolulu: Univ. Hawaii.

Conant, S. 1981. Birds. (Altitudinal distribution of organisms along an island mountain transect). In Island ecosystems: biological organization in selected Hawaiian communities, ed. D. Mueller-Dombois, R.W. Bridges, and H.L. Carson., 97-105. Stroudsburg, Penn.: Hutchinson Ross Pub. Co.

Conant, S. 1983. Red-vented bulbul alert. Elepaio 44 (4):38.

Cooray, R.G., and D. Mueller-Dombois. 1981. Feral pig activity. In Island ecosystems: biological organization in selected Hawaiian communities, ed. D. Mueller-Dombois, R.W. Bridges, and H.L. Carson, 309-317. Stroudsburg, Penn.: Hutchinson Ross Pub. Co.

Cox, P.A. 1983. Extinction of the Hawaiian avifauna resulted in a change of pollinators for the ieie, Freycinetia arborea. Oikos 41:195-199.

Diong, C.H. 1983. Population ecology and management of the feral pig (Sus scrofa L.) in Kipahulu Valley, Maui. Ph.D. Diss., Univ. Hawaii, Honolulu.

Dunmire, W.W. 1962. Bird populations in Hawaii Volcanoes National Park. Elepaio 22:65-70.

Flint, M.L., and R. van den Bosch. 1981. Introduction to integrated pest management. New York: Plenum Pr.

Gagne, B.H. 1982. Silversword alliance in the bogs of east Maui: a continuing report. Proc. 4th Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 62. Honolulu: Univ. Hawaii.

Gagne, W.C. 1980. Altitudinal distribution and composition of arthropods in ohia (Metrosideros collina subsp. polymorpha) canopies in Hawaii Volcanoes National Park with ecological implications for some native biota. Proc. 3rd Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 115-123. Honolulu: Univ. Hawaii.

Gagne, W.C., and C.C. Christensen. Conservation status of native terrestrial invertebrates in Hawaii. [This volume]

Giffin, J.G. 1978. Ecology of the feral pig on the island of Hawaii. Final Rep., Hawaii Dep. Land Nat. Resour., Pittman-Robertson Proj. W-15-3, Stud. 11. Mimeo.

Giffin, J.G. 1982. Ecology of the mouflon sheep on Mauna Kea. Final Rep., Hawaii Dep. Land Nat. Resour., Pittman-Robertson Proj. W-17-R, Stud. R-3. Mimeo.

Giffin, J.G. 1983. Alala investigations. Final Rep., Hawaii Dep. Land Nat. Resour., Pittman-Robertson Proj. W-18-R, Study R-II-B (1976-1981). Mimeo.

Giffin, J.G., J.M. Scott, and S. Mountainspring. In prep. Habitat relationships of the Hawaiian crow and preserve design. Hawaii Dep. Land Nat. Resour.

Gregg, W.P., Jr. 1984. The international network of biosphere reserves: A new dimension in global conservation. Pres. Miami Internatl. Symp. Biosphere, April. Miami Beach, Fla.

Handy, E.S.C., and E.G. Handy. 1972. Native planters in old Hawaii: their life, lore, and environment. B.P. Bishop Mus. Bull. 233.

Hawaii Division of Forestry and Wildlife. 1983. Hawaii wildlife plan. Honolulu: Hawaii Dep. Land Nat. Resour.

Higashino, P.K., and C.P. Stone. 1982. The fern jungle exclosure in Hawaii Volcanoes National Park: 13 years without feral pigs in a rain forest. [Abstract] Proc. 4th Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 86. Honolulu: Univ. Hawaii.

Holt, R.A., and B. Fox. Protection status of the native Hawaiian biota. [This volume]

Hood, G.A. 1978. Vertebrate control chemicals: current status of registrations, rebuttable presumptions against registrations, and effects on users. Proc. 8th Vert. Pest Control Conf., 170-176.

Howarth, F.G. 1983. Classical biocontrol: panacea or Pandora's box. Proc. Hawaii. Entomol. Soc. 24 (2&3):239-244.

Howarth, F.G. Impacts of alien land arthropods and mollusks on native plants and animals in Hawaii. [This volume]

Huffaker, C.B. 1975. Biological control in the management of pests. Agro-Ecosystems 2:15-31.

Imber, M.J. 1978. The effects of rats on breeding success of petrels. In The ecology and control of rodents in New Zealand nature reserves, ed. P.R. Dingwall, I.A.E. Atkinson, and C. Hay, 67-72. New Zealand Dep. Lands Surv. Info. Ser. 4. Wellington.

Jacobi, J.D. 1976. The influence of feral pigs on a native alpine grassland in Haleakala National Park. Proc. 1st Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 107-112. Honolulu: Univ. Hawaii.

Jacobi, J.D. 1980. Changes in a native grassland in Haleakala National Park following disturbance by feral pigs. Proc. 2nd Conf. Sci. Res. Natl. Parks. Vol. 8, 294-308. San Francisco, Calif.: Natl. Park Serv.

Kami, H.T. 1966. Foods of rodents in the Honokaa District, Hawaii. Pac. Sci. 20(3):367-373.

Katahira, L. 1980. The effects of feral pigs on a montane rain forest in Hawaii Volcanoes National Park. Proc. 3rd Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 173-178. Honolulu: Univ. Hawaii.

Kepler, C.B. 1967. Polynesian rat predation on nesting Laysan albatrosses and other Pacific seabirds. Auk 84:426-430.

King, W.B., and P.J. Gould. 1967. The status of Newell's race of the Manx shearwater. Living Bird 6:163-186.

Kirch, P.V. 1979. Subsistence and ecology. In The prehistory of Polynesia, ed. J.D. Jennings, 286-307. Cambridge, Mass.: Harvard Univ. Pr.

Kirch, P.V. 1982. The impact of the prehistoric Polynesians on the Hawaiian ecosystem. Pac. Sci. 36 (1):1-14.

Kirch, P.V., and D.E. Yen. 1982. Tikopia: the prehistory and ecology of a Polynesian outlier. B.P. Bishop Mus. Bull. 238.

Kobayashi, K. 1979. Court ruling gives palilas [sic] a lease on life. Honolulu Advertiser, June 7, p. A-3.

Kramer, R.J. 1971. Hawaiian land mammals. Rutland, Vt.: C.E. Tuttle Co.

Kridler, E. 1966. Experimental poisoning of the Hawaiian mongoose with thallium sulfate. U.S. Fish Wildl. Serv., Honolulu. Typescript.

La Rivers, I. 1948. Some Hawaiian ecological notes. Wasmann Collect. 7(3):85-110.

Lamoureux, C.H. Restoration of native ecosystems. [This volume]

Lewin, V. 1971. Exotic game birds of the Puu Waawaa Ranch, Hawaii. J. Wildl. Manage. 35(1):141-155.

Loope, L.L. 1982. The role of research in management of three tropical biosphere reserves in the United States. Pres. Indo.-U.S. Workshop Conserv. Biol. Diversity, Manage. Biosphere Reserves, Bangalore, India.

Loope, L.L. 1983a. Haleakala silversword: an optimistic note. Park Sci. 3(3):23-24.

Loope, L.L. 1983b. Resource management plan, Kipahulu District, Haleakala National Park. Natl. Park Serv. Typescript.

Loope, L.L., and P.G. Scowcroft. Vegetation response within exclosures in Hawaii: a review. [This volume]

McEldowney, H. 1979. Archaeological and historical literature search and research design. Lava flow control study, Hilo, Hawaii. Prep. U.S. Army Corp. Engineers, Contract DACW84-77-C-0019. B.P. Bishop Mus. Anthropol. Dep., Honolulu. Typescript.

McEldowney, H. 1983. A description of major vegetation patterns in the Waimea-Kawaihae region during the early historic period. Rep. 16. In Archaeological investigations of the Mudlane-Waimea-Kawaihae road corridor, island of Hawaii: an interdisciplinary study of an environmental transect, ed. J.T. Clark and P.V. Kirch, 407-448. B.P. Bishop Museum Dep. Anthropol. Rep. Ser. 83-1.

McNab, J. 1983. Wildlife management as scientific experimentation. Wildl. Soc. Bull. 11(4):397-401.

Moulton, M.P., and S.L. Pimm. 1983. The introduced Hawaiian avifauna: biogeographic evidence for competition. Am. Nat. 121(5):669-690.

Mountainspring, S., and J.M. Scott. In press. Interspecific competition among Hawaiian forest birds. Ecol. Monogr..

Mueller-Dombois, D. 1981. Vegetation dynamics in a coastal grassland of Hawaii. Vegetatio 46:131-140.

Mueller-Dombois, D. Ohia dieback and protection management of the Hawaiian rain forest. [This volume]

National Research Council. 1979. Nutrient requirements of swine. 8th ed. Washington, D.C.: Natl. Acad. Sci.

Olson, S.L., and H.F. James. 1982. Prodromus of the fossil avifauna of the Hawaiian Islands. Smithson. Contrib. Zool. 365.

Perkins, R.C.L. 1903. Vertebrata. In Fauna Hawaiiensis, ed. D. Sharp, Vol. I, pt. IV, 365-466. Cambridge, England: The Univ. Pr.

Pimm, S.L., and J.W. Pimm. 1982. Resource use, competition, and resource availability in Hawaiian honeycreepers. Ecology 63(5):1468-1480.

Pond, W.G., and K.A. Houpt. 1978. The biology of the pig. Ithaca, New York: Cornell Univ. Pr.

Ralph, C.J. 1978. Habitat utilization and niche components in some Hawaiian endangered forest birds. [Abstract] Proc. 2nd Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 238. Honolulu: Univ. Hawaii.

Rauzon, M.J. 1983. Feral cats of Jarvis Island: their effects on seabirds and their eradication. M.A. Thesis, Univ. Hawaii, Honolulu.

Ripperton, J.C., and E.Y. Hosaka. 1942. Vegetation zones of Hawaii. Hawaii Agric. Exp. Stn. Bull. 89.

Ruggiero, M., and G. Johnston. 1984. Pest management: the IPM approach. Park Sci. 4(2):22.

Russell, C.A. 1980. Food habits of the roof rat (Rattus rattus) in two areas of Hawaii Volcanoes National Park. Proc. 3rd Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 269-272. Honolulu: Univ. Hawaii.

Schmitt, R.C. 1971. New estimates of the pre-censal population of Hawaii. J. Polynesian Soc. 80(2): 237-243.

Schwartz, C.W., and E.R. Schwartz. 1949. The game birds in Hawaii. Honolulu: Hawaii Board Comm. Agric. For., Terr. Hawaii.

Scott, J.M., S. Mountainspring, F.L. Ramsey, and C.B. Kepler. In press. Forest bird communities of the Hawaiian Islands: their dynamics, ecology, and conservation. U.S. Fish Wildl. Serv. Stud. Avian Biol.

Scowcroft, P.G. 1983. Tree cover changes in mamane (Sophora chrysophylla) forests grazed by sheep and cattle. Pac. Sci. 37(2):109-119.

Scowcroft, P.G., and J.G. Giffin. 1983. Feral herbivores suppress mamane and other browse species on Mauna Kea, Hawaii. J. Range Manage. 36(5):638-645.

Shallenberger, R.J. 1981. Hawaii's birds. 3rd ed. Honolulu: Hawaii Audubon Soc.

Simons, T.R. 1983. Biology and conservation of the endangered Hawaiian dark-rumped petrel (Pterodroma phaeopygia sandwichensis). Univ. Wash. Coop. Natl. Park Resour. Stud. Unit Tech. Rep. 83-2. Seattle: Univ. Wash.

Singer, F.J. 1981. Wild pig populations in the National Parks. Environ. Manage. 51(3):263-270.

Smith, C.W. Impact of alien plants on Hawaii's native biota. [This volume]

Smith, J.D., and J.R. Woodworth. 1951. A study of the pheasant, California quail, and lace-necked dove in Hawaii. Hawaii Fish Game Div. Spec. Bull. 3.

Spatz, G., and D. Mueller-Dombois. 1973. The influence of feral goats on koa tree reproduction in Hawaii Volcanoes National Park. Ecology 54(4):870-876.

Spatz, G., and D. Mueller-Dombois. 1975. Succession patterns after pig diggings in grassland communities on Mauna Loa, Hawaii. Phytocoenologia 3(2/3):346-373.

Stone, C.P. 1984. National Park Service research and management to control introduced animals in Hawaii. Trans. 24th Ann. For. Wildl. Conf., 68-80. Honolulu.

Stone, C.P., and D.D. Taylor. 1984. Status of feral pig management and research in Hawaii Volcanoes National Park. Proc. 5th Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 106-117. Honolulu: Univ. Hawaii.

Stone, C.P., P.C. Banko, P.K. Higashino, and F.G. Howarth. 1984. Interrelationships of alien and native plants and animals in Kipahulu Valley, Haleakala National Park: a preliminary report. Proc. 5th Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 91-105. Honolulu: Univ. Hawaii.

Stone, C.P., R.L. Walker, J.M. Scott, and P.C. Banko. 1983. Hawaiian goose management and research: where do we go from here? Elepaio 44(2):11-15.

Tomich, P.Q. 1969. Mammals in Hawaii: a synopsis and notational bibliography. Honolulu: Bishop Mus. Pr.

Tomich, P.Q. 1981. Rodents. (Altitudinal distribution of organisms along an island mountain transect). In Island ecosystems: Biological organization in selected Hawaiian communities, ed. D. Mueller-Dombois, R.W. Bridges, and H.L. Carson, 105-110. Stroudsburg, Penn.: Hutchinson Ross Pub. Co.

Tuggle, H.D. 1979. Hawaii. In The prehistory of Polynesia, ed. J.D. Jennings, 167-199. Cambridge, Mass.: Harvard Univ. Pr.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47(4): 893-901.

van Riper, C., III. 1976. The influence of food supplementation upon the reproductive strategy and movement patterns in the Hawaii amakihi (Loxops virens). Proc. 1st Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 227. Honolulu: Univ. Hawaii.

van Riper, C., III. 1980. The phenology of the dryland forest of Mauna Kea, Hawaii, and the impact of recent environmental perturbations. Biotropica 12(4):282-291.

van Riper, C., III. 1984. The influence of nectar resources in nesting success and movement patterns of the common amakihi (Hemignathus virens). Auk 101(1):38-46.

van Riper, S.G., and C. van Riper III. 1982. A field guide to the mammals in Hawaii. Honolulu: Oriental Pub. Co.

van Riper, S.G., and C. van Riper III. A summary of known parasites and diseases recorded from the avifauna of the Hawaiian Islands. [This volume]

Vitousek, P.M., K. Van Cleve, and N. Balakrishnan. In press. Soil development and nitrogen turnover in montane rainforests soils on Hawaii. Biotropica.

Vitousek, P.M., W.A. Reiners, J.M. Meilillo, C.C. Grier, and J.R. Gosz. 1981. Nitrogen cycling and loss following forest perturbation: the components of response. In Stress effects on natural ecosystems, ed. G.W. Barrett and R. Rosenburg, 115-127. New York: John Wiley Sons, Ltd.

Vitousek, P.M., J.R. Gosz, C.C. Grier, J.M. Meilillo, W.A. Reiners, and R.L. Todd. 1979. Nitrate losses from disturbed ecosystems. Science 204:469-474.

Wagner, W.L., D.R. Herbst, and R.S.N. Yee. Studies of the native flowering plants of the Hawaiian Islands. [This volume]

Warshauer, F.R., J.D. Jacobi, A.M. LaRosa, J.M. Scott, and C.W. Smith. 1983. The distribution, impact and potential management of the introduced vine Passiflora mollissima (Passifloraceae) in Hawaii. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. 48. Honolulu: Univ. Hawaii.

Williams, J. 1980. Native vs exotic woody vegetation recovery following goat removal in the eastern coastal lowlands on Hawaii Volcanoes National Park. Proc. 3rd Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 373-382. Honolulu: Univ. Hawaii.

Williams, R.N. 1983a. Bulbul introductions on Oahu. Elepaio 43(11):89-90.

Williams, R.N. 1983b. The red-vented bulbul on the island of Hawaii. Elepaio 43(12):101-103.

Wilson, F., and C.B. Huffaker. 1976. The philosophy, scope and importance of biological control. In Theory and practice of biological control, ed. C.B. Huffaker and P.S. Messenger, 3-15. Internatl. Organ. Biol. Control, Internatl. Ctr. Biol. Control. New York: Academic Pr.

Woodworth, J.R., and D.H. Woodside. 1953. Mongoose poison experiment. Terr. Hawaii Pittman-Robertson Job Complet. Rep. Proj. 5-R-4, Work Plan 4, Job 29 (4), 1-16. Typescript.

A SUMMARY OF KNOWN PARASITES AND DISEASES RECORDED FROM THE AVIFAUNA OF THE HAWAIIAN ISLANDS

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ABSTRACT

Introduced parasites and diseases are among the many threats which confront the continued existence of native Hawaiian landbirds. These birds are infected with a variety of endemic parasites, and many new parasites have arrived in Hawai'i via introduced birds. There is evidence today which suggests that disease is playing a role in limiting the numbers and distributions of native birds. To better understand the interactions of parasites with their hosts, a myriad of native and introduced disease-causing organisms must be identified.

This paper presents a summary of the recorded parasites and diseases in Hawaiian birds. Each disease-causing organism is discussed in terms of its characteristics of infection and pathogenicity, life cycle and intermediate hosts, and avian hosts in Hawai'i. The disease records and references are categorized taxonomically and by avian host. Most diseases appear to be of little concern to biologists worried about the preservation of Hawaiian birdlife. However, at least 2 have been important in the past (avian pox and malaria), and others could be equally important in the future. It is, therefore, imperative that the impact of the disease threat be recognized, and that steps be taken to properly deal with this situation in the Islands. Recommendations are given for future directions that disease research might pursue, and for possible monitoring and control methods for extant and potential newly arriving diseases.

INTRODUCTION

More than 20 million years ago, molten lava rose from the ocean depths to form the first Hawaiian island. Volcanic activity constantly added new material to replace eroded land, leaving today an island chain extending more than 5,000 kilometers across the Pacific and rising in places to heights greater than 9,000 m from the ocean floor. Sporadic biological colonization relying principally on the trade winds and ocean currents led to the evolution of many endemic land and fresh-water bird species, including 3 unique subspecies of sea birds. Colonizing birds brought compliments of parasites to these remote islands. Today the biological complexity is enhanced as new infectious organisms continue to arrive and interact with native and introduced bird species.

The first avian parasites to reach the Hawaiian Islands undoubtedly arrived with early migrant birds. In recent times there has been a tremendous influx of new arrivals, and consequently the number of parasites and diseases has also increased. Most diseases hold little threat to well established populations, and indeed may support the ecological balance and stability of the host population. However, when confronted with newly encountered diseases, the native birds often become more severely infected than their introduced counterparts.

The situation of differential species susceptibility has been documented in North American birds, where introduced avian species succumb more readily to the native eastern equine encephalitis virus than do native birds (Karstad 1971). A similar case may be made for avian malaria in Hawai'i (van Riper et al., in press; Warner 1968), where native birds are more susceptible to this introduced parasite. Of special note is the fact that many extant populations of Hawaiian birds are small, and when population numbers are not sufficient to sustain fluctuations caused by disease outbreaks, the threat of extinction is enhanced.

In order to preserve and properly protect the Hawaiian avifauna, it is imperative that the impact of disease be recognized, and that proper steps be taken to adequately deal with it. The procurement of baseline data showing which avian diseases are currently present in Hawai'i is especially important. The purpose of this paper is to catalog the known information on parasites and disease factors recorded in wild Hawaiian birds. Captive and domesticated birds are considered only where transmission to wild populations is possible (e.g., domestic chickens, turkeys, some zoo birds, and pigeons). Scientific names of birds not given in the text are given in the Appendix. Each disease is discussed in terms of its individual characteristics of infection and pathogenicity, life cycle, and avian hosts in Hawai'i; and records of parasites and diseases are summarized in the Appendix. Confusing reports have been omitted, as have many cases of parasites not identified to genus or species.

CLASSIFICATION OF PARASITES REPORTED FROM HAWAIIAN BIRDS

The taxonomic classification given below is based on information from the following sources: Baker and Wharton 1952; Bequaert 1941; Goff 1980; Goff and van Riper 1980; Keymer 1982b; Krantz 1978; Kudo 1966; Levine 1980, 1982a, 1982b; Levine, van Riper, and van Riper 1980; Lewin and Holmes 1971; McDonald 1981; Rothschild and Clay 1957; Turner 1971; Wardle, McLeod, and Radinovsky 1974. Synonyms used in reference to Hawaiian birds are given in parentheses.

Phylum: Protozoa
- Order: Rhizomastigida
  - Family: Mastigamoebidae
    - *Histomonas meleagridis*
- Order: Trichomonadida
  - Family: Trichomonadidae
    - *Trichomonas gallinae* (= *T. columbae*)
- Order: Coccidida
  - Family: Eimeriidae
    - *Eimeria tenella*
    - *Isospora ivensae*
    - *Isospora brayi*
    - *Isospora phaeornis*
    - *Isospora loxopis*
    - *Isospora vanriperorum*
  - Family: Atoxoplasmatidae
    - *Atoxoplasma* sp.
- Order: Haemosporida
  - Family: Plasmodiidae
    - *Plasmodium relictum*
  - Family: Haemoproteidae
    - *Haemoproteus columbae*

Phylum: Nematoda
- Order: Strongylorida
  - Family: Syngamidae
    - *Syngamus trachea*
  - Family: Trichostrongylidae
    - *Amidostomum* sp. (= *Amidospomen*)
    - *Ornithostrongylus quadriradiatus*
- Order: Ascaridorida
  - Family: Heterakidae
    - *Ascaridia galli*
    - *Ascaridia perspicillum*
    - *Ascaridia* sp.
    - *Aulonocephalus pennula*
    - *Heterakis gallinarum* (= *H. papillosa* = *H. gallinae*)
    - *Heterakis* sp.

Family: Ascarididae
Porrocaecum semiteres
Porrocaecum ensicaudatum
Family: Subuluridae
Subulura brumpti
(= Allodapa brumpti)
Subulura skrjabinensis
Subulura sp.
Order: Spirurorida
Family: Spiruridae
Cyrnea graphophasiani
Microtetrameres sp.
Procyrnea longialatus
Tetrameres americana
(= Tropisurus americanus)
Tetrameres sp.
Family: Acuariidae
Cheilospirura hamulosa
(= Acuaria hamulosa)
Cheilospirura sp.
Dispharynx nasuta (= D. spiralis)
Dispharynx sp.
Synhimantus
(= Dispharynx zosteropsi)
Viguiera hawaiiensis
Family: Thelaziidae
Gongylonema ingluvicola
Oxyspirura mansoni
Oxyspirura sp.
Order: Dorylaimorida
Family: Trichuridae
Capillaria sp.

Phylum: Acanthocephala
Order: Echinorhynchidea
Family: Plagiorhynchidae
Plagiorhynchus charadrii
Order: Gigantorhynchidea
Family: Gigantorhynchiidae
Mediorhynchus orientalis

Phylum: Cestoda
Order: Davaineidea
Family: Davaineidae
Fuhrmannetta crassula
(= Raillietina crassula)
Raillietina cesticillus
(= Davainea cesticillus)
Raillietina tetragona
(= Davainea tetragona)
Raillietina sp.
Order: Hymenolepididea
Family: Hymenolepididae
Hymenolepis carioca

(= *Echinolepis carioca*;

= *Davainea carioca*)

Hymenolepis megalops

(= *Cloacotaenia megalops*)

Orientolepis exigua

(= *Hymenolepis exigua*;

= *Hymenosphenacanthus exiguus*)

Order: Dilepididea

Family: Paruterinidae

Anonchotaenia brasilense

Family: Dipylidiidae

Choanotaenia infundibulum

(= *C. infundibuliformis*)

Family: Dilepididae

Metroliasthes lucida

Phylum: Trematoda

Order: Strigeatoidea

Family: Schistosomatidae

Austrobilharzia variglandis

Family: Brachylaemidae

Postharmostomum gallinum

Urotocus rossittensis

Order: Echinostomida

Family: Philophthalmidae

Philophthalmus gralli

Order: Opisthorchiida

Family: Heterophyidae

Centrocestus formosanus

Haplorchis taichui

Haplorchis yokogawai

Phylum: Arthropoda

Class: Arachnida

Subclass: Acari

Order: Parasitiformes

Suborder: Ixodida

Family: Argasidae

Ornithodoros capensis

Ornithodoros denmarki

Family: Ixodidae

Haemaphysalis wellingtoni

Ixodes laysanensis

Suborder: Gamesida

Family: Rhinonyssidae

Mesonyssus geopeliae

Neonyssus sp.

Paraneonyssus sp.

Ptilonyssus hirsti

(= *Haemolaelaps casalis*)

Ptilonyssus sp.

Rhinonyssus coniventris

Rhinonyssus sp.

Sternostoma tracheacolum

Family: Dermanyssidae
Dermanyssus gallinae
Family: Macronyssidae
Ornithonyssus bursa
(= *Liponyssus bursa*)
Ornithonyssus sylviarum
(= *Liponyssus sylivaun*)
Ornithonyssus sp.
Family: Laelapidae
Androlaelaps sp.
Haemolaelaps fenilis
(= *H. megaventralis*;
= *Atricholaelaps megaventralis*;
= *H. casalis*)
Suborder: Actinedida
Family: Cheyletidae
Bakericheyla chanayi
Cheyletus malaccensis
Cheyletus eruditus
Cheyletus sp.
Family: Cheylettiellidae
Neocheyletiella media
(= *Ornithochyla* sp.)
Ornithocheyletia leiothrix
Family: Ereynetidae
Boydaia agelaii
Boydaia nigra
Opthalmognathus tenorioae
Family: Harpyrhynchidae
Harpyrhynchus pilirostris
Harpyrhynchus sp.
Family: Trombiculidae
Eutrombicula conantae
Guntherana domrowi
Leptotrombidium intermedium
Neoschoengastia gallinarum
Neoschoengastia ewingi
Neoschoengastia gettmanni
Neotrombicula tamiayi
Schoengastia pobsa
Toritrombicula nihoaensis
Toritrombicula oahuensis
Suborder: Acaridida
Family: Pyroglyphidae
Dermatophagoides evansi
Family: Analgidae
Analges sp.
Anhemialges sp.
Megninia columbae
Megninia cubitalis
Megninia ginglymura
Megninia sp.
Mesalgoides sp.
Onychalges sp.

Ornithocheyla sp.
Strelkovarius sp.
Family: Dermoglyphidae
Dermoglyphus elongatus
Falculifer rostratus
Gabucinia delibatus
Gabucinia sp.
Pterolichus obtusus
Pterolichus sp.
Pteronyssus sp.
Xoloptes sp.
Family: Proctophyllodidae
Montesauria sp.
Proctophyllodes longiphyllus
Proctophyllodes vegetans
Proctophyllodes pinnatus
Proctophyllodes truncatus
Proctophyllodes sp.
Pterodectes sp.
Pteroherpus oxyplax
Family: Sarcoptidae
Knemidokoptes mutans
Mesoknemidocoptes laevis
(= *Knemidokoptes laevis*)
Family: Cytoditidae
Cytodites nudus
Family: Pteronyssidae
Mouchetia sp.
n. gen., n. sp.
Family: Trouessartiidae
Calcealges sp.
Calcealges yunkeri
Trouessartia sp.
Family: Xolalgidae
Ingrassiella sp.
n. gen., n. sp.
Family: Hypoderidae
Neottialges fregatae
Neottialges hawaiiensis
Class: Insecta
Order: Mallophaga
Family: Menoponidae
Actornithophilus epiphanes
Actornithophilus kilauensis
Actornithophilus milleri
Amyrsidea monostoecha
Austromenopon infrequens
Austromenopon sternophilum
Colpocephalum brachysomum
Colpocephalum discrepans
Colpocephalum hilensis
Colpocephalum turbinatum
Longimenopon puffinus
Machaerilaemus hawaiiensis

Menopon sp.
Menopon gallinae
Menopon fulvomaculatum
Menopon phaeostomum
Menacanthus spinosus
Menacanthus stramineus
Myrsidea sp.
Myrsidea cyrtostigma
Myrsidea incerta
Myrsidea invadens
Trinotin querquedulae
Uchida sp.

Family: Philopteridae

Anaticola crassicorne
Bruelia stenzona
Bruelia vulgata
Columbicola columbae
Columbicola sp.
Chelopistes meleagridis
Cuclotogaster heterographa
Docophoroides sp.
Goniocotes asterocephalus
Goniocotes bidentatus
Goniocotes chinensis
Goniocotes gallinae
Goniocotes hologaster
Goniodes sp.
Goniodes colchici
Goniodes dissimilis
Goniodes gigas
Goniodes lativentris
Goniodes mammillatus
(= G. mammilatus)
Halipeurus mirabilis
Harrisoniella sp.
Lagopoecus colchicus
Lagopoecus docophoroides
Lipeurus caponis
Lipeurus maculosus
Lunaceps sp.
Oxyliperus polytrapezius
Philopterus macgregori
Philopterus subflavescens
Quadraceps birostris
Quadraceps connexa
Quadraceps oraria
Quadraceps separata
Rallicola advena
Saemundssonia conicus
Saemundssonia snyderi
Trabeculus (= Giebelia) mirabilis

Order: Siphonaptera

Family: Pulicidae

Echidnophaga gallinacea

Order: Diptera

Family: Hippoboscidae

Icosta (= *Lynchia*) *nigra*
Olfersia aenescens
Olfersia spinifera
Ornithoctona hulahula
Ornithoica vicina (= *O. pusilla*)
Pseudolynchia canariensis

Family: Culicidae

Aedes aegypti
Aedes albopictus
Aedes vexans
Culex quinquefasciatus

ENDOPARASITES

Protozoa

Histomonas

Infection Characteristics: *Histomonas meleagridis* is a well-known and economically important parasite of gallinaceous birds, characterized by necrosis of the liver and ulceration of the caecum. It causes the disease "blackhead," which is typically less pathogenic in chickens than in turkeys (Kemp and Springer 1978).

Life Cycle: In captive turkeys and chickens, blackhead is usually passed from bird to bird within the ova of the nematode *Heterakis gallinarum* (Ruff 1978). Mechanical transmission may also be accomplished via earthworms, flies, grasshoppers, sowbugs, and crickets (Kemp and Springer 1978).

Hawaiian Hosts: *Histomonas meleagridis* has been reported in Hawai'i only from domestic chickens and turkeys (Alicata 1964). While transmission to wild gallinaceous birds is possible, it does not seem to be prevalent in Hawai'i.

Trichomonas

Infection Characteristics: *Trichomonas gallinae* is the only trichomonad known to cause mortality in wild birds. It infects primarily the mouth, throat, and crop, and secondarily the liver, lungs, heart, and other internal organs (Kocan and Herman 1971). Death may result from destruction of host tissue, or by mechanical blockage of the throat which ultimately results in starvation. The lesions in the mouth may superficially resemble aspergillosis, candidiasis, or avian pox, so any diagnosis must differentiate among these 4 maladies. This is not a common parasite of wild birds. However, it has been known to cause severe epidemics in wild populations of mourning doves (*Zenaidura macroura*) in Alabama (Haugen 1952), and should an epizootic of trichomoniasis occur in Hawai'i, it could have catastrophic results (Kocan and Banko 1974).

Life Cycle: Transmission of Trichomonas is direct, with parasites transferred during the feeding of young or during courtship feeding, particularly when regurgitation is involved. Eating of contaminated food is also a means of transmission (Kocan and Herman 1971). Some species of native Hawaiian birds feed their young by regurgitation (van Riper 1978, 1980), so there is the potential for transmission.

Hawaiian Hosts: Trichomonas gallinae was first reported in Hawai'i from 2 individuals in a flock of Signal Corps pigeons (Yeager and Gleiser 1946). Since that time there have been very few instances of this disease noted in the Islands. Smith and Guest (1974) captured one nutmeg mannikin at Diamond Head, O'ahu, that later died of Trichomonas after a period of time in an aviary. The only wild birds to be discovered with trichomoniasis in Hawai'i have been 2 zebra doves captured by Kocan and Banko (1974) and one 'apapane that we captured by mist net on the island of Hawai'i (unpubl. data).

Coccidia (Eimeria and Isospora)

Infection Characteristics: Most of the information known about coccidiosis comes from studies of poultry, but at least 5 genera of intestinal coccidia infect wild birds: Eimeria, Isospora, Dorisiella, Wenyonella, and Tyzzeria (Todd and Hammond 1971). Coccidia are very host specific. Generally the degree of pathogenicity varies in individuals, causing inflammation and destruction of intestinal tissue, diarrhea, and often dehydration. Young animals are the most severely affected, and coccidia have been implicated in the mortality of young quail and grouse (Bennett, Greiner, and Threlfall 1976; Herman, Jankiewicz, and Saarni 1942). Immunity increases with exposure and older individuals often serve as reservoirs (Todd and Hammond 1971).

Life Cycle: Coccidia are intestinal protozoans with a direct life cycle. The protozoans are shed with fecal material and survive best in warm, humid conditions (Reid 1978b). In captivity, transmission is accomplished via contaminated food or water (Todd and Hammond 1971). Little is known about transmission in the wild.

Hawaiian Hosts: Unfortunately, the genera of coccidia have seldom been differentiated in Hawaiian parasite surveys, and such reports of wild birds include the Japanese white-eye (Guest 1973), zebra dove, northern mockingbird (Mimus polyglottos), red-crested cardinal, house sparrow, blue-capped cordonbleu, red-cheeked cordonbleu (Uraeginthus bengalus), lavender waxbill, and orange-cheeked waxbill (Smith and Guest 1974). Captive birds with coccidiosis from the Honolulu Zoo, University of Hawai'i, Paradise Park, and other areas include the 'anianiau, common 'amakihi, northern cardinal, and Hawaiian goose or nene (A. Miyahara, pers. comm.; Honolulu Zoo 1964-1967 necropsy records). Eimeria tenella is a common parasite in fowl and has been identified from chickens (Alicata 1964). Five new species of Isospora were recently described from birds on the island of Hawai'i (Levine, van Riper, and van Riper 1980). Seventeen of 59 Japanese white-eyes were positive for Isospora bravi, 3 of 15 nutmeg mannikins carried Isospora ivensae, one of 11 Hawaiian thrushes had Isospora phaeornis, 3 of 24 common 'amakihi had Isospora loxopis, and one northern cardinal examined had Isospora vanriperorum (Levine 1982a). In addition, we found 2 'apapane and one 'elepaio infected with Isospora sp. from the island of Hawai'i (unpubl. data).

Atoxoplasma

Infection Characteristics: Atoxoplasma is a protozoan parasite that infects the white blood cells of passerine birds. This disease is relatively nonpathogenic and some avian populations have chronic infection rates of 100% with few adverse signs (Lainson 1959).

Life Cycle: Atoxoplasma has been incorrectly referred to in the past as avian toxoplasmosis, and a controversy exists concerning the life cycle and taxonomy of this parasite. It is felt by some (Lainson 1959, 1960) that mites, in particular Dermanyssus gallinae, are responsible for transmission, and that the genus should be Lankesterella. However, Box (1970, 1971, 1977) provided evidence that Atoxoplasma may be a stage of the intestinal coccidian Isospora. More complete reviews may be found in Baker et al. (1972) and Levine (1982b).

Hawaiian Hosts: Atoxoplasma was unknown in Hawai'i until 1978, when it was discovered in a house sparrow (van Riper et al., in press). Of 70 house sparrows examined on the island of Hawai'i, 9% were infected, as were 17.4% of 121 nutmeg mannikins. In addition, several house finches that we held in captivity were positive for Atoxoplasma (unpubl. data).

Plasmodium

Infection Characteristics: Avian malaria in Hawai'i is caused by the protozoan parasite Plasmodium relictum. This parasite infects peripheral red blood cells and internal tissue such as liver, spleen, bone

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Haemoproteus

Infection Characteristics: *Haemoproteus columbae* is a common parasite of rock doves throughout the world and is often referred to as "pigeon malaria." The sexual stages of this parasite infect the red blood cells, while all stages develop in endothelian cells of blood vessels in the lungs, liver, spleen, and other internal organs (Cook 1971a). Most *Haemoproteus* infections have not been reported as being severely pathogenic to their hosts, and some rock dove populations have infection rates up to 100%, with few adverse overt signs being exhibited by the birds (Levine and Kantor 1959).

Life Cycle: *Haemoproteus* is transmitted by members of the Hippoboscidae (louse flies) and/or *Culicoides* (biting midges) (Cook 1971a). The common pigeon hippoboscid, *Pseudolynchia canariensis*, is the vector of *H. columbae*. The sexual stages of the protozoan take place within the insect, and infection is accomplished when the fly bites another bird.

Hawaiian Hosts: *Haemoproteus columbae* is present in Hawai'i in both wild and captive rock doves (Alicata 1964; Kartman 1949; Navvab Gojrati 1970; Yeager and Gleiser 1946). In a 1978 survey we conducted of 230 pigeons from the Honolulu Zoo, over 98% were infected with *Haemoproteus* (unpubl. data). Warner (1968) reported a possible infection of house finches and an 'apapane with *Haemoproteus*, but the parasite was probably misidentified (Laird and van Riper 1981).

Leucocytozoon

Infection Characteristics: *Leucocytozoon* occurs only in birds, and it has a worldwide distribution. After an acute stage following initial infection, most cases become chronic with occasional relapses when the avian host is under stress (Cook 1971b).

Life Cycle: These blood parasites primarily develop within leukocytes and occasionally in erythrocytes. They multiply in epithelian and other cells. The intermediate hosts are blackflies of the family Simuliidae (Cook 1971b).

Hawaiian Hosts: *Leucocytozoon* has been reported only once in Hawai'i (Navvab Gojrati 1970), and this was probably an error (Laird and van Riper 1981). The vectors of this parasite are absent from the Islands (Crosskey, in press); therefore, this parasite does not at present constitute a serious threat to the Hawaiian birds.

Nematoda

Syngamus

Infection Characteristics: *Syngamus trachea*, or the gapeworm, is usually encountered in the trachea, although the bronchi may also be infected (Wehr 1971). The worms feed on blood, causing mechanical damage and production of mucus where they attach to the tissue. Young birds seem most seriously affected, with clinical signs being gaping, coughing, and pneumonia-like symptoms (Levine 1980). The lumen of the trachea may become obstructed, and the bird suffocates (Wehr 1971).

Life Cycle: The life cycle of *Syngamus trachea* may be direct or include an earthworm or other invertebrate which the parasite utilizes as a transport host. This parasite has been found in earthworms as long as 3.5 years after ingestion (Levine 1980).

Hawaiian Hosts: *Syngamus trachea* has been reported in wild birds only on O'ahu: one red-crested cardinal (Smith 1973b) and one house finch (Smith and Guest 1974).

Ornithostrongylus

Infection Characteristics: *Ornithostrongylus quadriradiatus* is found in rock doves worldwide (Wehr 1971). This parasite infects the small intestine, feeding on blood (Ruff 1978). In some instances it may appear in a very acute form and produce many fatalities (Wehr 1971).

Life Cycle: Eggs are shed in the feces and transmission is accomplished via fecal contamination (Ruff 1978).

Hawaiian Hosts: *Ornithostrongylus quadriradiatus* has been reported only from rock doves in Hawai'i. Alicata (1939a, 1964) believed that this parasite was responsible for general unthriftiness and losses among the rock doves in the Islands.

Amidostomum

Infection Characteristics: Members of this genus often infect Anseriformes and are usually found under the horny lining of the gizzard (Levine 1980). The Canada goose gizzard worm *Amidostomum anseris* causes considerable mortality in young birds, as well as inhibiting growth and development of those that survive. According to Herman and Wehr (1954), *A. anseris* itself is not a primary source of loss but rather an important contributing factor.

Life Cycle: The life cycle of the Hawaiian parasite is unknown but *A. anseris* has a direct life cycle. Eggs are shed in feces and larvae penetrate the skin or are eaten (Levine 1980).

Hawaiian Hosts: Amidostomum sp. was reported from a wild Hawaiian goose (Banko and Manuwal 1982), but unfortunately no specific identification of the worm was made.

Heterakis

Infection Characteristics: Members of the genus Heterakis are common parasites of Galliformes and occasionally of captive geese and ducks (Wehr 1971). These parasites are usually found in the caecum, although the small intestine may also be infected. They live on intestinal contents and do not migrate during their development, so damage to the host is minimal (Levine 1980). Heterakis gallinarum is the vector of the protozoan Histomonas meleagridis, which causes blackhead in chickens and turkeys (Ruff 1978).

Life Cycle: Eggs are shed in feces and infect a bird when they are ingested. Sowbugs and earthworms may also ingest ova and carry them for long periods of time, facilitating transmission to birds (Levine 1980).

Hawaiian Hosts: In Hawai'i, H. gallinarum has been reported in domestic chickens and other wild game birds (Alicata 1964; Guberlet 1926; Lewin and Holmes 1971; Schwartz and Schwartz 1949, 1951; Swanson 1939). Banko and Manuwal (1982) reported a species of Heterakis from wild Hawaiian geese. Avery (1966) reported H. dispar in captive Hawaiian geese at Slimbridge, England. Possibly this is the parasite observed by Banko and Manuwal.

Aulonocephalus

Infection Characteristics: The ascarid Aulonocephalus pennula is a common parasite of quail from the southwestern United States, and it is not very pathogenic to its host. It is usually found in the caecum and occasionally in the small intestine (Lewin and Holmes 1971).

Life Cycle: The life cycle is unknown (Lewin and Holmes 1971).

Hawaiian Hosts: Aulonocephalus pennula has been reported from the California quail in Hawai'i (Lewin and Holmes 1971). This constituted a new host record and is the only report of this parasite in the Islands.

Ascaridia

Infection Characteristics: Ascaridia worms are common and are often a serious problem in poultry, causing retardation of growth, constipation or diarrhea, and loss of condition. These large roundworms are found in the intestine, which may be blocked by heavy infections. Ascarids have also been found to augment the effects of other diseases such as coccidiosis, Heterakis, and infectious bronchitis (Levine 1980; Ruff 1978), probably by lowering the host's general resistance.

Life Cycle: The life cycle of this helminth does not require an intermediate host (Wehr 1971), although eggs may be ingested by grasshoppers or earthworms and in turn infect an avian host when the invertebrate is eaten. The eggs hatch in the host's proventriculus or upper intestine and the larvae cause destruction and hemorrhaging of the intestinal mucosa during migration (Ruff 1978).

Hawaiian Hosts: Ascaridia galli and A. perspicillum have been reported from domestic chickens (Alicata 1964; Guberlet 1926; Swanson 1939) and Ascaridia sp. from ring-necked pheasants and spotted doves (Schwartz and Schwartz 1949, 1951). Alicata (1964) thought that the pheasant ascarid infection reported by Schwartz and Schwartz (1949) was probably A. galli.

Porrocaecum

Infection Characteristics: Adult Porrocaecum worms reside in the intestine, where they feed on large quantities of blood. These parasites cause subnormal weight, vomiting, and severe anemia (Wehr 1971).

Life Cycle: All members of this genus require intermediate hosts such as earthworms (Wehr 1971). In one study from North America, 60% of the earthworms in soil covered with bird droppings contained infective P. ensicaudatum larvae (Levine 1980).

Hawiian Hosts: Two members of this genus have been reported from Hawai'i: Porrocaecum semiteres and P. ensicaudatum, both from the lesser golden plover (Okimoto 1975).

Subulura

Infection Characteristics: Members of the genus Subulura infect a variety of birds, usually Galliformes, but occasionally Anseriformes, Columbiformes or other wild birds (Levine 1980). Adult worms reside in the caecum or small intestine, where little damage to the host occurs (Wehr 1971).

Life Cycle: Little is known about the life cycle of species of Subulura in the wild (Wehr 1971), but Subulura brumpti, a common parasite of poultry, requires an intermediate host (Alicata 1939b). In Hawai'i these include any of the following: the beetles Alphitobius diaperinus, Ammophorus insularis, Dermestes vulpinus, Gonocephalum seriatum, and Tribolium castaneum; the grasshoppers Conocephalus saltator and Oxya chinensis; and the dermapter Euborellia annulipes (Cuckler and Alicata 1944).

Hawaiian Hosts: Subulura brumpti has been recorded in Hawai'i from the gray francolin, Barbary partridge, Japanese quail, ring-necked pheasant, California quail, domestic chicken, wild turkey, and spotted dove (Alicata 1939b; Lewin and Holmes 1971; Schwartz and Schwartz 1951). Subulura skrjabinensis has been recorded from the Pacific golden plover (Okimoto 1975), and Subulura sp. (possibly S. brumpti) in chickens, ring-necked pheasants, and Japanese quail (Schwartz and Schwartz 1949; Swanson 1939).

Cyrnea and Procyrnea

Infection Characteristics: These helminth groups infect the proventriculus but apparently do not cause serious damage to their hosts (Levine 1980).

Life Cycle: All of the Cyrnea and Procyrnea species require intermediate hosts. The host of C. graphophasiani is unknown, but other species of Cyrnea (e.g. C. colina) can utilize the German cockroach (Blatella germanica) (Levine 1980; Cram 1931), which is present in Hawai'i.

Hawaiian Hosts: Cyrnea graphophasiani was reported from ring-necked pheasants (Schwartz and Schwartz 1951). This is the only member of this genus reported from the Islands and constituted a new host record for the parasite. It has not subsequently been recorded in the Islands. Procyrnea longialatus, a new species, was collected from the proventriculus of Japanese white-eyes and 'apapane from the island of Hawai'i (Cid del Prado Vera, Maggenti, and van Riper, in press).

Tetrameres and Microtetrameres

Infection Characteristics: Both Tetrameres and Microtetrameres are found primarily in the proventriculus (Wehr 1971) and are known as globular stomach worms. Some species produce severe pathology because they require extensive blood to produce eggs (Wehr 1971). T. americana, the species which infects chickens, is well studied and very important in the poultry industry (Alicata 1964).

Life Cycle: Throughout the world, various species of Tetrameres utilize amphipods, grasshoppers, cockroaches, and earthworms as intermediate hosts. In Hawai'i Tetrameres americana utilizes grasshoppers (Conocephalus saltator and Oxya chinensis), and the

German cockroach as intermediate hosts (Cram 1931; Kartman 1951). The intermediate hosts of Microtetrameres in Hawai'i are unknown.

Hawaiian Hosts: Mitrotetrameres sp. has been reported in Hawai'i from the Japanese white-eye (Smith and Guest 1974) and Tetrameres sp. from the rock dove, red-crested cardinal, house sparrow, lavender waxbill, and common 'amakihi (Alicata 1964; Kartman 1951; Smith and Guest 1974; van Riper 1975). But without knowing what species are present in Hawai'i, it is difficult to predict the effect of infections on host populations. Tetrameres americana infects domestic poultry in the Islands (Alicata 1964).

Cheilospirura

Infection Characteristics: Cheilospirurads are generally found in gallinaceous birds. The worms live beneath the gizzard lining, causing severe deterioration of this organ (Wehr 1971).

Life Cycle: The beetles Tenebroides nana and Epitragus diremptus, and the sandhopper Orchestia platensis all serve as naturally infected intermediate hosts in Hawai'i (Alicata 1938b). Experimental intermediate hosts include the beetles Carpophilus dimidiatus, Dactylosternum abdominale, Dermestes vulpinus, Epitragus diremptus, Euxestus sp., Gonocephalum seriatum, Litargus balteatus, Oxydema fusiforme, Palorus ratzeburgi, Sitophilus oryzae, Tenebroides nana, Tribolium castaneum, and Typhaea stercorea; the grasshoppers Atractomorpha ambigua, Conocephalus saltator, and Oxya chinensis; and the amphipod Orchestia platensis (Alicata 1947, 1964).

Hawaiian Hosts: The first report in Hawai'i of Cheilospirura hamulosa was by Swanson (1939) in domestic chickens. Schwartz and Schwartz (1949) reported Cheilospirura sp. in the ring-necked pheasant, and in 1951 they identified C. hamulosa from the same host. Domestic turkeys also harbor C. hamulosa (Alicata 1964).

Dispharynx and Synhimantus

Infection Characteristics: Dispharynx nasuta has a worldwide distribution and has been reported from a variety of columbiform, galliform, and passeriform birds (Wehr 1971). It is a common parasite of the proventriculus, esophagus, and rarely, the intestine (Levine 1980). D. nasuta causes deep ulcerations and becomes almost buried under proliferating tissue (Levine 1980). Considerable losses have been recorded in ruffed grouse (Bonasa umbellus) from the United States, with young birds being most severely affected (Wehr 1971). In a survey of birds in New York City, the parasite was found to be pathogenic mainly in gallinaceous birds, with catbirds (Dumetella carolinensis) being the only passerine species obviously affected (Goble and Kutz 1945). However, some pigeon populations also experience heavy losses from this parasite (Hwang et al. 1961).

Life Cycle: All members of Dispharynx and Synhimantus require an intermediate host. The intemediate host of D. nasuta in Hawai'i is the sowbug Porcellio laevis (Alicata 1964). Eggs hatch inside the sowbug and become infective after 26 days. The life cycle of S. zosteropsi is unknown.

Hawaiian Hosts: In Hawai'i Dispharynx nasuta has been reported from California quail, Barbary partridge, domestic chickens, turkeys, and pigeons (Alicata 1964; Lewin and Holmes 1971). Dispharynx sp. has also been reported in the common myna, red-crested cardinal, and northern cardinal (Smith and Guest 1974). We found a species of Dispharynx in zebra doves from the Honolulu Zoo. All could well have been D. nasuta. The closely related species Synhimantus zosteropsi is being described from the gizzard of Japanese white-eyes on the island of Hawai'i (Cid del Prado Vera, Maggenti, and van Riper, in press).

Viguiera

Infection Characteristics: Members of the genus Viguiera infect the proventriculus and gizzard, and in heavy infections the erosion of the tissue may be severe. These worms are worldwide in distribution (Cram 1927).

Life Cycle: All members of Viguiera require an intermediate host. Many spiruroirids utilize arthropods (Levine 1980), but the hosts for Viguiera in Hawai'i are unknown.

Hawaiian Hosts: Viguiera hawaiiensis, a new species, was collected from between the gizzard tunic layers of the 'apapane, common 'amakihi, and 'i'iwi on the island of Hawai'i (Cid del Prado Vera, Maggenti, and van Riper, in press).

Oxyspirura

Infection Characteristics: The distribution of Oxyspirura mansoni, the common eyeworm, includes a wide variety of hosts worldwide. This worm infects primarily Galliformes, Columbiformes, and Passeriformes (Ruff 1978). Adult worms are found beneath the nictitating membrane of the eye, causing lesions which vary from mild conjunctivitis to severe ophthalmia (Levine 1980).

Life Cycle: The intermediate host of Oxyspirura mansoni in Hawai'i, and worldwide, is the burrowing cockroach *Pycnoscelus surinamensis* (Schwabe 1951). The propensity of birds to eat cockroaches and cockroach availability are probably the limiting factors in this parasite's distribution. The maintenance of giant toads (*Bufo marinus*) has been advocated as a means of cockroach control (Alicata 1947).

Hawaiian Hosts: *Oxyspirura mansoni* is the most commonly reported parasitic nematode in Hawai'i, and it has been found in the following introduced avian species: Barbary partridge, gray francolin, bare-throated francolin, Japanese quail, Kalij pheasant, domestic chicken, ring-necked pheasant, wild turkey, California quail, spotted dove, zebra dove, common myna, red-crested cardinal, and house sparrow (Alicata 1936, 1964; Eddinger 1967; Illingsworth 1931; Lewin and Holmes 1971; Schwartz and Schwartz 1949, 1951; Smith and Guest 1974; Swanson 1939). We found rock doves at the Honolulu Zoo to be occasionally infected (unpubl. data). In addition, a second, unidentified species of *Oxyspirura* was found in California quail and bare-throated francolin (Lewin and Holmes 1971).

Gongylonema

Infection Characteristics: *Gongylonema ingluvicola* is known as the common poultry cropworm. It produces only local lesions without serious pathological effects to the crop (Ruff 1978).

Life Cycle: The beetle *Copris minutis* serves as an intermediate host in the continental United States and in Hawai'i; the beetle *Copris incertus* is also a suitable host (Alicata 1964).

Hawaiian Hosts: In Hawai'i *Gongylonema ingluvicola* has been reported from ring-necked pheasants (Swanson 1939) and domestic chickens (Alicata 1939a).

Capillaria

Infection Characteristics: Capillarid worms usually cause extensive damage to their hosts because adults feed directly on blood and tissue. The intestinal lining may be destroyed and absorption capabilities greatly decreased (Wehr 1971).

Life Cycle: Some *Capillaria* species have direct life cycles, while others require intermediate hosts, such as earthworms (Levine 1980; Wehr 1971). The capillarids in Hawai'i have not been determined to species, and their life cycles are unknown.

Hawaiian Hosts: *Capillaria* sp. has been reported in the northern cardinal, blue-capped cordonbleu, orange-cheeked waxbill (Smith and Guest 1974), and common 'amakihi (van Riper 1975). We have found a species of *Capillaria* in 'apapane and 'i'iwi from the island of Hawai'i (unpubl. data). Cid del Prado Vera, Maggenti, and van Riper (in press) reported a species of *Capillaria* from the 'apapane. Captive common 'amakihi from Paradise Park also harbor a capillarid (A. Miyahara, pers. comm.).

Acanthocephala

Infection Characteristics: Acanthocephalans, or thorny-headed worms, are found in the intestines of many vertebrates, especially fish, where they cause inflammation at the site of attachment. Anemia and/or enteritis is common, and in some cases the gut lining may be completely perforated (Schmidt 1969).

Life Cycle: The life cycles of acanthocephalans in Hawai'i are undetermined, but all require one or more intermediate hosts. These hosts may include various arthropods, vertebrates (lizards or amphibians), or annelids (Ruff 1978).

Hawaiian Hosts: Smith and Guest (1974) found *Plagiorhynchus charadrii* and *Mediorhynchus* sp. in lesser golden plovers, and the latter in a common myna, red-crested cardinal, and northern cardinal. Okimoto (1975) reported *Plagiorhynchus charadrii* and *Mediorhynchus orientalis* from golden plovers, and Schmidt and Kuntz (1977) collected *M. orientalis* larvae from a golden plover. Although only reported in Hawai'i from plovers, *M. orientalis* seems to prefer passerine species as hosts (Schmidt and Kuntz 1977). The only acanthocephalan reported from a native passerine was identified as *Apororhynchus hemignathi* in the 'akialoa by Perkins (1903).

Cestoda

Tapeworms are common parasites of birds. Unfortunately, many reports from Hawai'i merely record "tapeworms" without specific identification. While this information is of note, it is of little value in determining the overall picture of parasite distributions in the Islands. These records include: rock dove (Schwartz and Schwartz 1949; Yeager and Gleiser 1946); spotted dove (Smith and Guest 1974); common myna (Guberlet 1926--2 species; Smith and Guest 1974); red-crested cardinal (Smith and Guest 1974); red-cheeked cordonbleu (Smith and Guest 1974); lavender waxbill (Smith and Guest 1974); 'akepa (Perkins 1903); and house sparrow (Smith and Guest 1974); common 'amakihi, 'apapane, and 'i'iwi (Baldwin 1948).

Raillietina

Infection Characteristics: Two members of *Raillietina* have been reported in Hawai'i, *R. cesticillus* and *R. tetragona*. There have been reports of *R.*

cesticillus causing pathology and reduced growth in poultry, but controlled experiments have failed to substantiate this. Reid (1978a) stated that perhaps modern optimal nutritional formulas may account for this disparity. On the other hand, R. tetragona has been shown to cause weight loss and a decrease in egg production which is more apparent in some breeds of chickens than others. R. cesticillus embeds in the duodenum and jejunum, while R. tetragona usually inhabits the posterior half of the intestine (Reid 1978a).

Life Cycle: Intermediate hosts in Hawai'i as listed by Alicata (1964) are: R. cesticillus--the beetles Dermestes vulpinus and Gonocephalum seriatum; R. tetragona--probably various species of ants, especially Pheidole sp. and Tetramorium sp.

Hawaiian Hosts: In Hawai'i, Raillietina cesticillus and R. tetragona are common in chickens (Alicata 1964), and an unidentified species of Raillietina has been recovered from pigeons (Yeager and Gleiser 1946).

Fuhrmannetta

Infection Characteristics: Fuhrmannetta tapeworms are characteristic of Columbiformes and occasionally Galliformes (Lewin and Holmes 1971). Their pathogenicity is unknown.

Life Cycle: The life history is unknown.

Hawaiian Hosts: Fuhrmannetta crassula was reported from California quail by Lewin and Holmes (1971), a first record for this species. They also speculated that the cestode in the spotted dove reported by Schwartz and Schwartz (1949) was Fuhrmannetta crassula.

Hymenolepis

Infection Characteristics: Hymenolepis carioca and H. megalops are well-known parasites of poultry and waterfowl (Reid 1978a). H. carioca is reportedly one of the least pathogenic tapeworms. The pathogenicity of H. megalops is largely unknown, although in England there are cases of severe mortality in ducks when this species is present in combination with H. coronula and H. furcigera (Reid 1978). Neither of these 2 species has been observed in Hawai'i. Interestingly, H. megalops is one of the few tapeworms that attach to the cloaca or bursa Fabricius instead of to the intestinal wall proper.

Life Cycle: Alicata (1964) listed the intermediate hosts for Hymenolepis carioca as the beetle Aphodius granarius and the fly Stomoxys calcitrans in Hawai'i. However, Reid (1978a) doubted that flies carry this parasite and stated that hosts throughout the world include many beetles and a termite. The life history of H. megalops is unknown.

Hawaiian Hosts: Hymenolepis carioca was reported from chickens by Guberlet (1926), and later from the same host by Alicata (1964). Hymenolepis megalops was found in Hawaiian ducks (Alicata 1964).

Orientolepis

Infection Characteristics: Members of this genus are closely related to Hymenolepis. One species has been reported from Hawai'i, Orientolepis exigua. Its pathogenicity is unknown.

Life Cycle: The amphipod Orchestia platensis serves as the intermediate host of this tapeworm in Hawai'i (Alicata and Chang 1939).

Hawaiian Hosts: Orientolepis exigua is common in chickens in Hawai'i (Alicata 1964) and has been recovered once from wild turkeys (Lewin and Holmes 1971).

Anonchotaenia

Infection Characteristics: Members of the bird family Fringillidae in North and South America and the Hawaiian Drepanidinae are the most common hosts of this genus of tapeworms (Vogue and Davis 1953). The pathogenicity is unknown.

Life Cycle: The life cycle of Anonchotaenia is unknown.

Hawaiian Hosts: Anonchotaenia brasilense was first recovered from the common 'amakihi, 'i'iwi, and 'apapane by P. Baldwin in 1948 and was later identified by Vogue and Davis (1953). We have recovered this tapeworm from the same species (unpubl. data). Perkins (1903) reported Drepanidotaenia hemignathi from an 'akialoa, and this may have been A. brazilense.

Choanotaenia

Infection Characteristics: Choanotaenia infundibulum is a common parasite of chickens throughout the world. It is a large, robust species which attaches to the upper half of the intestine. There have been no controlled experiments to determine its pathogenicity (Reid 1978a).

Life Cycle: The intermediate hosts of C. infundibulum in Hawai'i include the beetles Dermestes vulpinus, Epitragus diremptus, and Gonocephalum seriatum, and the house fly Musca domestica (Alicata 1964). Throughout the world a wide variety of insects (beetles, grasshoppers, termites) have been shown to be experimental hosts (Reid 1978a).

Hawaiian Hosts: Choanotaenia infundibulum was first identified in Hawai'i from chickens by Guberlet (1926), and this was later confirmed by Alicata (1938a). Lewin and Holmes (1971) also reported this parasite from Barbary partridge, Japanese quail, and California quail.

Metroliasthes

Infection Characteristics: Metroliasthes lucida is a long tapeworm often found in turkeys, guinea fowl, and sometimes chickens. The pathogenicity of this species is unknown (Reid 1978a).

Life Cycle: Throughout the world, grasshoppers serve as the intermediate host for M. lucida (Ruff 1978).

Hawaiian Hosts: Metroliasthes lucida was found in wild Hawaiian turkeys (Lewin and Holmes 1971). This is the only report of this tapeworm in Hawai'i.

Trematoda

Austrobilharzia

Infection Characteristics: Austrobilharzia variglandis is a blood fluke found in mesenteric veins of avian hosts, although larval dermatitis in humans has been reported (Chu and Cutress 1954).

Life Cycle: This fluke utilizes the littorine snail Littorina pintado as an intermediate host in Hawai'i (Alicata 1964). Eggs hatch in water into miracidia which penetrate the snail host. After maturation, cercariae are released and penetrate the skin of the final host (Noble and Noble 1971).

Hawaiian Hosts: Chu and Cutress (1954) reported the schistosome fluke, Austrobilharzia variglandis, from a ruddy turnstone.

Postharmostomum

Infection Characteristics: Postharmostomum gallinum is a cecal fluke of galliform and columbiform birds worldwide. It causes inflammation and hemorrhage in the caecum, and it is a common parasite of chickens raised on the ground (Alicata 1964).

Life Cycle: The land snail Bradybaena similaris is the first and second intermediate host; the land snail Subulina octona may also serve as a second intermediate host in Hawai'i (Alicata 1940). Birds become infected by eating snails containing metacercariae.

Hawaiian Hosts: Alicata (1940) reported this cecal fluke in chickens from Hawai'i.

Urotocus

Infection Characteristics: Urotocus rossittensis is a cosmopolitan species, found in a variety of passerine hosts worldwide (Williams 1960). The flukes are almost always located in the bursa Fabricius. The organ becomes distended when infected.

Life Cycle: The life cycle is unknown, but in one drepanid that we found with a fluke infection, the land snail Tornatellaria was recovered from the crop contents. This snail may serve as an intermediate host to the fluke, but more study is needed.

Hawaiian Hosts: One 'amakihi and 2 'apapane from a sample of 60 birds on Hawai'i were infected with Urotocus rossittensis (unpubl. data). Van Riper (1975) reported a "fluke" in common 'amakihi, which was probably this species.

Philophthalmus

Infection Characteristics: Philophthalmus gralli is a small trematode which occurs in the eyes of game birds throughout the world. The infection results in congestion and erosion of the conjunctiva (Kingston 1978).

Life Cycle: The melanid snails Thiara granifera and Stenomelania newcombi serve as intermediate hosts for eye flukes in Hawai'i. The cercariae encyst on any solid object including snail shells or crayfish exoskeletons. When the snail or crayfish is eaten, the metacercariae migrate to the eye of the final host (Alicata 1962, 1969; Alicata and Ching 1960; Ching 1961).

Hawaiian Hosts: The eye fluke has been observed in Hawaiian coots and cattle egrets (Alicata 1969).

Centrocestus and Haplorchis

Infection Characteristics: Flukes in the family Heterophyidae normally live in the small intestine and cause little harm. Some pain or diarrhea may result from the infections, and occasionally the eggs may find their way into the blood and cause mild to serious trouble in the organs into which they infiltrate (Noble and Noble 1971).

Life Cycle: Heterophyid flukes utilize melanid snails and fish as first and second intermediate hosts, respectively. Martin (1958) determined that the fresh water snail Stenomelania newcombi serves as the first intermediate host for Centrocestus formosanus and

Haplorchis yokogawai. The snail Tarebia granifera is the first intermediate host of Haplochis taichui. In Hawai'i, the fish Mugil cephalus, Gambusia affinis, or Xiphophorus helleri serve as a second host for Centrocestus formosanus and Haplochis taichui. H. taichui also utilizes the fish Mollienesia formosus. Haplochis yokogawai was not recovered from any free-living intermediate hosts, but Martin speculated that hosts are probably the mullet (Mugil cephalus) and the Chinese catfish (Clarias fuscus).

Hawaiian Hosts: Martin (1958) reported three heterophyid flukes (Centrocestus formosanus, Haplorchis taichui, and H. yokogawai) from the black-crowned night heron in Hawai'i. Besides this bird, cats and rats will serve as final hosts, and all 3 fluke species will infect man if infected raw fish is eaten. Okimoto (1975) reported a heterophyid fluke in a lesser golden plover but gave no further description of the parasite.

ECTOPARASITES

Ectoparasites are found on the body or feathers of their avian host, for part or all of the parasite's life cycle. We have included among the ectoparasites the respiratory mites, although many species are actually found internally in the lungs, air sacs, or even embedded within the internal organs. Because of the numbers of ectoparasites and paucity of information on the infection characteristics of some species, we have discussed these parasites by order, suborder, and family in most cases rather than by genus as in the endoparasites. Moreover, the subsections of "Infection Characteristics" and "Life Cycle" have been condensed into one.

Acari

Ixodida Ticks

Infection Characteristics and Life Cycle: Ticks are the largest of the parasitic Acarina. They typically frequent nests, intermittently feeding on their hosts during all of the parasite's life stages. Heavy infestation can lead to severe host anemia, nest desertion, and even death (Baker and Wharton 1952). In addition, a number of arboviruses have been isolated from ticks (Brennan 1965). Tick eggs are laid in the nest or near the ground. The larvae feed on the host, molting into nymphs which in turn feed on the host before assuming adult form. Some ticks require several hosts at various stages to complete their life cycles (Baker and Wharton 1952).

Hawaiian Hosts: Only 3 species of ticks have been reported from wild birds in the Hawaiian Islands: Ornithodoros capensis, O. denmarki (soft ticks), and

Ixodes laysanensis (hard ticks). Ticks have been reported from the black-footed and Laysan albatrosses, wedge-tailed and Townsend's shearwaters, brown noddy, ruddy turnstone, and Laysan duck (Butler 1961; Butler and Usinger 1963; Wilson 1964a; Kohls, Sonenshine, and Clifford 1965). Ornithodoros capensis is generally abundant on Laysan, Kure, Pearl and Hermes Reef, Lisianski, Gardner, Necker, Nihoa, and French Frigate Shoals (Garrett and Haramoto 1967). However, the parasite has, in many cases, been in the nest rather than directly on the host when collected. Haemaphysalis wellingtoni was recovered from a pheasant from Thailand at the Honolulu Quarantine Station, but there is no evidence of this parasite being established in Hawai'i (Garrett and Haramoto 1967).

Gamasida Mites

Infection Characteristics and Life Cycle: The Gamasida mites are a heterogeneous taxonomic group and include some of the most notorious pathogenic mites, including the Rhinonyssidae, Dermanyssidae, and Macronyssidae. The Rhinonyssidae, or bird nasal mites, are found internally within the air sacs and respiratory system, and even embedded in the internal organs and peritoneum of their hosts. These mites can cause severe respiratory distress (Arnall and Keymer 1975). Little is known about respiratory mites, but they probably spend entire life cycles on or in their host (Keymer 1982b). Dermanyssus gallinae, the red mite, is one of the best known of the Dermanyssidae. It feeds at night, hiding near roosts during the day. It is common among poultry and a variety of wild and cage birds. D. gallinae can cause weight loss, anemia, and even death (Keymer 1982b) and has been implicated in the transmission of Atoxoplasma (Lainson 1960), eastern equine encephalomyelitis (Howitt et al. 1948), and trypanosomes (Macfie and Thompson 1929; Manwell and Johnson 1931). Another mite that sucks blood and can cause similar serious problems is Ornithonyssus sylviarum (Macronyssidae). While this species appears uncommonly on wild birds, this may not be an accurate reflection of the true distribution because it visits the host only for feeding, and therefore might be missed during surveys (Goff 1980). The Laelapidae are usually parasitic (Baker and Wharton 1952) and have also been implicated in disease transmission (Krantz 1978).

Hawaiian Hosts: Gamasida mites have been reported from individuals or the nests of the following avian species in Hawai'i: Hawaiian crow, zebra dove, house sparrow, 'amakihi, nutmeg mannikin, golden plover, lavender waxbill, blue-headed cordonbleu, orange-cheeked waxbill, red-eared waxbill, domestic chicken, common myna, house finch, and 'apapane (see the Appendix for a complete mite species list with references).

Actinedida Mites

Infection Characteristics and Life Cycle: Actinedida mites are a very diverse group, cosmopolitan in distribution, and found in all habitat types (Krantz 1978). Cheyletidae mites are usually free-living predators, although they are found on the bodies of birds and sometimes appear to injure the host (Baker and Wharton 1952). The Harpyrhynchidae are generally parasitic. They are found in or under the cuticles of birds, and most of the specimens that have been recovered in Hawai'i were found in body washes of birds (Goff 1980). Trombiculidae (chiggers) cause irritation to their hosts, and some release toxins that may result in allergic reactions (Arnall and Keymer 1975). Chiggers feed on their hosts only as larvae and are free-living predators as nymphs and adults, feeding on small arthropods in the soil (Baker and Wharton 1952).

Hawaiian Hosts: Mites of the suborder Actinedida have been identified from the following Hawaiian birds or their nests: Japanese white-eye, red-billed leiothrix, house sparrow, common 'amakihi, 'apapane, 'i'iwi, Laysan finch, ruddy turnstone, brown noddy, black-crowned night heron, black-footed and Laysan albatross, and golden plover (see Appendix for references). In addition, mites identified only to the family Syringophilidae were reported from the quills of common 'amakihi, palila, 'elepaio, and Japanese white-eye (Berger 1981).

Acaridida Mites

Infection Characteristics and Life Cycle: This group includes various species of feather mites from the Analgidae, Dermoglyphidae, Trouessartiidae, Proctophyllodidae, Pyroglyphidae, Sarcoptidae, Pteronyssidae, Cytoditidae, and Xolalgidae. The feather mites, as a rule, are not harmful to their hosts. They are scavengers, feeding on feather debris and dead skin (Evans, Sheals, and MacFarlane 1961; Krantz 1978). However, in some cases heavy infestation may lead to feather picking. We have found several 'apapane with abnormally high infestations of feather mites and deformed beaks, suggesting the importance of preening in the control of these parasites. Each group of feather mites has a distinct local preference upon the surface or within the quills (Krantz 1978), and remains with the host for the entire parasite life cycle. An Acaridida nest mite that causes little effect on the host is Dermatophagoides, which feeds mainly on detritus in the nest and is only occasionally found on birds (Krantz 1978). The specimens collected in Hawai'i were considered nonparasitic (Goff 1980). Sarcoptid mites of the genera Mesoknemidocoptes and Knemidokoptes are many times a problem in caged birds. These ectoparasites cause severe irritation to individuals, referred to as scaly leg and scaly face (Keymer 1982b). Sarcoptid mites have not yet been recovered from wild Hawaiian birds. Cytodites nudus is a common air sac and respiratory mite of chickens, with pathogenesis varying from mild to severe (Loomis 1978). Little is known about the incidence, life cycle, or effects of Cytodites in wild birds (Keymer 1982b).

Hawaiian Hosts: Feather mites have been reported from the ring-necked pheasant, rock dove, spotted dove, domestic chicken, 'anianiau, Japanese white-eye, common myna, nutmeg mannikin, Hawaiian crow, Hawaiian thrush, 'apapane, 'i'iwi, common 'amakihi, millerbird, California quail, Japanese quail, northern cardinal, and house finch (see Appendix for a complete list of references). Other Acaridida in Hawai'i include Dermatophagoides (Pyroglyphidae) from the house sparrow (Goff 1980); Knemidokoptes and Mesoknemidocoptes (Sarcoptidae) from the chicken (Bice 1932); a new species of Mouchetia (Pteronyssidae) described from the Japanese white-eye and 'apapane, and one species yet to be determined from the red-billed leiothrix (Goff 1980); 2 members of the Xolalgidae (Ingrassiella) from common 'amakihi and 'i'iwi; a new as yet unnamed species from the short-eared owl (Goff 1980); Cytodites nudus (Cytoditidae) from the chicken (Bice 1932); and Cytodites sp. from a red-billed leiothrix (Goff 1980).

Insecta

Mallophaga

Infection Characteristics: Mallophaga, or feather lice, feed primarily on feathers or scavenged debris from feather surfaces; they may also take blood, serum, and skin tissues. Some species effectively puncture young feathers and feed on the central pulp and blood, while other species penetrate the shafts of mature feathers and feed on the dried feather core (Rothschild and Clay 1957). Generally, harm to the host is minimal except in very heavy infections (Ash 1960), especially when blood-sucking species are involved. Bathing, preening, and other grooming behaviors help to eliminate lice. Mallophaga are not important carriers of disease although at least one louse in swifts serves as an intermediate host to a filarian (Noble and Noble 1971), and eastern equine encephalomyelitis has been isolated from another species (Howitt et al. 1948); however, neither has been reported from Hawai'i. Birds generally have several species of lice, and young birds tend to have heavier loads than do adults (Rothschild and Clay 1957).

Life Cycle: The entire life cycle of Mallophaga is spent on the host (Keymer 1982b). Eggs are attached directly to feathers, and several nymphal stages develop prior to emergence of the adult form. Lice cannot live for more than a few days away from the host.

Hawaiian Hosts: Mallophaga have been reported from a variety of species of birds of Hawai'i (see Appendix for host list and references). Indeed, probably all avian species are infected with at least one type of louse (Rothschild and Clay 1957).

Siphonaptera

Infection Characteristics: Echidnophaga gallinacea has a wide range of hosts in tropical and subtropical areas (Rothschild and Clay 1957). It is commonly known as the stick-tight flea, and unlike most fleas, remains embedded in the skin of the host, usually about the head. Adults feed on blood and can cause irritation, anemia, and even death in heavy infections (Turner 1971). Fleas have not been implicated in the transmission of other avian diseases (Loomis 1978).

Life Cycle: The eggs are forcibly ejected and reach the litter where the larvae hatch and feed on organic material (Loomis 1978). After a pupal stage, the adult form is assumed.

Hawaiian Hosts: Only one species of flea, Echidnophaga gallinacea, has been reported from Hawai'i. It was found on the domestic chicken (Illingsworth 1916) and the California quail (Schwartz and Schwartz 1949, 1951).

Hippoboscidae

Infection Characteristics: Hippoboscid flies are capable of flight but usually cling to the bird's feathers, moving rapidly over the body and feeding periodically on blood. Hippoboscids cause anemia, especially in heavy infections on very small birds (Keymer 1982b). They can also act as an intermediate host for other parasites. Pseudolynchia canariensis, the common pigeonfly, carries Haemoproteus, a blood protozoan. Ornithoica vicina is a very common hippoboscid fly on birds from North America, particularly passerines, and is common throughout the Pacific islands (Bequaert 1941). Olfersia are common flies of seabirds and are widespread throughout the Pacific and Atlantic. Icosta nigra is usually found on birds of prey in North America.

Life Cycle: Eggs are laid in the nest, but the adults remain near or on their host for most of the life cycle (Keymer 1982b).

Hawaiian Hosts: There have been several species of Hippoboscidae reported from birds in Hawai'i;

white-eye, northern cardinal, and 'elepaio (W. Hansen, pers. comm.). Therefore, the many reports of "lesions" may indeed be a true reflection of the picture of avian pox in the Islands, but more substantiation is needed.

Newcastle disease

Infection Characteristics: Domestic poultry that are infected with Newcastle disease exhibit coughing, lowered productivity, leg and wing paralysis or other nervous symptoms, diarrhea, hemorrhage, and death (Hanson 1978). Very little is known about the pathogenesis in wild birds (Palmer and Trainer 1971).

Transmission: This disease is extremely contagious, being transmitted via contact with sick birds or their droppings (Hanson 1978). It has been reported to be carried by the mite Dermanyssus gallinae (Palmer and Trainer 1971) and other invertebrates such as earthworms (Boyd and Hanson 1958).

Hawaiian Hosts: Newcastle disease was introduced accidentally to Hawai'i from California in July 1977 by an infected parrot. In 1979 a ban on importation of all live birds from California to Hawai'i was imposed on the State (Berger 1981). The disease has never been reported from wild Hawaiian birds, and a survey of 17 wild birds and 599 captive birds for Newcastle disease in 1980 was negative (U.S. Department of Agriculture and Southeastern Cooperative Wildlife Disease Study 1980), although the disease was later reported from Hilo in 1981.

Arboviruses or togaviruses

Infection Characteristics: There are several arboviruses that constitute a threat to a wide variety of domestic and wild birds (Buescher 1956; Coleman 1978; Hammon, Sather, and McClure 1958; Karstad 1971). Many infected individuals remain asymptomatic carriers (Kissling et al. 1954), although the disease is often fatal, with neurological signs predominating, including muscular tremors and degrees of paralysis (Cavill 1982).

Transmission: Arboviruses are transmitted chiefly by mosquitoes, and secondarily by other arthropods such as mites, lice, ticks, and directly from bird to bird (Brennan 1965; Cavill 1982; Howitt et al. 1948; Sulkin and Izumi 1947).

Hawaiian Hosts: Both the American (eastern equine encephalitis, western equine encephalitis, St. Louis encephalitis) and the Asian types (Japanese B encephalitis virus) could reach Hawai'i. Several surveys of birds in Hawai'i have indicated that these arboviruses are not yet present in the Islands

(Quisenberry and Wallace 1959; Wallace et al. 1964), but several potential vectors (Aedes spp., Culex quinquefasciatus, and various mites) are.

Bacterial Diseases

Infection Characteristics: Bacterial diseases are common and often a high percent are fatal. In many cases, disease is caused by a bacterium that is usually commensal. Stress of other disease factors can easily upset the physiological balance and lead to bacterial infections. In birds, enteritis is commonly associated with Escherichia coli, Staphylococcus, Salmonella, Pseudomonas aeruginosa, Pasteurella, or Yersinia; septicemic diseases are related to Salmonella, E. coli, Pseudomonas, Streptococcus, Staphylococcus, or Pasteurella; and respiratory diseases such as pneumonia are often associated with E. coli, Salmonella, Klebsiella, Corynebacterium, Pseudomonas, and Staphylococcus (T-W-Fiennes 1982). Botulism, a paralytic disease, is caused by eating food contaminated by the toxin produced by the bacterium Clostridium botulinum. Death is due to paralysis of the respiratory and/or cardiac muscles. Many deaths from this disease occur in waterfowl, shorebirds, or game birds if conditions are conducive (Rosen 1971).

Transmission: Transmission of bacterial diseases varies but generally occurs via contact with sick or carrier individuals, or through contaminated material. Botulism is found naturally in the soil, but when water levels drop and temperatures are high, the organism multiplies in dead organic material and releases a toxin. The organic material may be decaying vegetation, various invertebrates (e.g. maggots), or vertebrates (e.g. fish). The toxin is nearly always fatal when ingested by birds.

Hawaiian Hosts: Most of the information on bacterial infections in Hawaiian birds is fragmentary. While many of the bacteria reported are not normally recognized as pathogenic, several of the types that have been identified are potentially serious pathogens. Staphylococcus was diagnosed as the cause of death of several Laysan finches in an outbreak at the Honolulu Zoo (Throp 1970). It began as a swelling on the tarsus of one bird and rapidly spread throughout the colony, causing many deaths. The birds showed little resistance to the bacterium, although Staphylococcus is ubiquitous and normally found on the skin. It is not unreasonable to assume that other native birds might also be susceptible to this bacterium. We also found Staphylococcus to be a problem in captive Laysan finches, and at least 2 individuals had Staphylococcus infections when they died in our aviary.

Escherichia coli and Salmonella have also been implicated in disease in wild birds. We discovered an 'apapane on the island of Hawai'i that had been killed by a cat; it had liver lesions typical of E. coli, and the gall bladder was distended and swollen. E. coli was isolated from both the liver and gall bladder. Salmonella was isolated from a wild palila from Mauna Kea that died after one night in an aviary. The bird had an enlarged heart and inflamed pericardium. In addition, we have been able to determine the presence of several other bacteria in the birds on the island of Hawai'i. Most of the following examples were probably not pathogenic (T.R. Sawa, pers. comm.). From Laysan finches, alpha and beta Streptococcus, Pseudomonas aeruginosa, Klebsiella pneumoniae, Serratia marcescens, Staphylococcus epidermis, and Citrobacter diversus were isolated. One house finch had Escherichia coli, and pancreatic lesions were evident in the bird. All of these birds were captive individuals. From the following wild birds we isolated the following bacteria: palila - Salmonella; 'i'iwi - Staphylococcus epidermis and Citrobacter fruendii; 'elepaio - alpha Streptococcus; 'apapane - Klebsiella pneumoniae, Escherichia coli, Pseudomonas pseudoalcaligens, and Enterobacter cloacae.

There has been only one recorded outbreak of botulism in Hawai'i, at Ka'elepulu Pond (Enchanted Lakes), O'ahu, in 1953 (Brock and Breese 1953). The infected species were primarily northern pintail and northern shoveler ducks. Other species included the American wigeon, American coot, black-necked stilt, greater scaup, black-crowned night heron, green-winged teal, and bufflehead.

Fungal Diseases

Aspergillus

Infection Characteristics: Avian aspergillosis is caused by the fungus Aspergillus fumigatus (Raper, Fennell, and Austwick 1973). It can assume either a chronic or acute form and usually infects the upper respiratory tract or abdominal organs (Keymer 1982a). The pathogenesis in wild birds is almost unknown, but in captive individuals where it is a common problem, the disease is often fatal and almost always incurable (O'meara and Witter 1971a).

Transmission: The spores of this fungus are very common and are present in most areas of the world. Most birds have been exposed and are resistant. In fact, the fungus can often be isolated from healthy tissue. It is contracted by inhalation of the spores or hyphae, and infection tends to be related to the age and physiological state of the bird (very young birds seem to be more susceptible) and number of spores inhaled (Keymer 1982a; O'meara and Witter 1971a).

Hawaiian Hosts: Aspergillus has been reported from several captive species in Hawai'i but has been infrequently found in wild birds. We found it in a wild Hawaiian thrush and common 'amakihi (unpubl. data). The thrush died less than 24 hours after capture, but in the common 'amakihi there were no apparent lesions or disease symptoms. Infected captive birds include the nene (Honolulu Zoo necropsy records, 1964), Hawaiian owl (Honolulu Zoo necropsy records, 1967), and common 'amakihi (Honolulu Zoo necropsy records, 1966). Probably all species of Hawaiian birds are susceptible if the conditions are conducive for infection.

Candida

Infection Characteristics: Candida albicans infects the digestive tract or respiratory system, causing lesions and inflammation. It is very rare in wild birds (O'meara and Witter 1971b).

Transmission: Transmission is accomplished via contaminated food or water, or by inhalation of the spores. The fungus is very widespread, so there appears to be more than ample opportunity for contact by wild birds (O'meara and Witter 1971b).

Hawaiian Hosts: Candidiasis has been reported only from captive birds in Hawai'i. 'Apapane harbor Candida albicans (A. Miyahara 1969 necropsy records), and we discovered one Laysan finch that was infected with this fungus (unpubl. data).

DISCUSSION

The isolation of the Hawaiian Islands has led to disharmonic patterning of biological species, and avian parasites and disease-causing organisms are no exception. Major taxonomic groups (protozoans, various helminths, ectoparasites, viruses, bacteria, fungi) are represented. However, within broad categories, many diseases are absent. This is especially true for bacteria and viruses. Prehistoric colonizing birds undoubtedly brought a spectrum of parasites with them, and these have coevolved with their hosts. Other parasites arrived concomitantly with the importation of alien birds, and this process is ongoing. Today biologists are faced with an array of parasites interacting with a unique assemblage of birds. Besides the simple cataloguing of what is present in Hawai'i, research is needed to determine the impact of each disease and the means of controlling or eradicating it if necessary. This discussion will deal with 3 points:

1. The difference between the threats posed by host-specific versus generalized diseases;

2. Examples of 2 non-specific diseases that have negatively influenced native birds; and,

3. Suggestions for directions of future research on avian diseases in Hawai'i.

The majority of parasites infecting Hawaiian birds fall into the host-specific category, infecting primarily one preferred host or related species. These usually cause mild, self-limiting infections, because parasites are most successful when causing the least trauma. A dramatic example of this is Haemoproteus in rock doves: incidence of infection includes nearly all of the population, and individual birds, which have very high parasitisms, show few adverse signs. Another example is coccidia in the native drepanids. Several endemic species have been described, but rarely are infections seen in the wild that cause overt symptoms. Host-specific parasites seldom significantly interrupt the life cycle of the host upon which they depend to complete their life cycle, although parasite trauma may be increased when multiple infections occur. For example, the presence of Ascaridia in birds augments the pathology of concurrent infections of coccidia, Heterakis, and infectious bronchitis (Levine 1980; Ruff 1978). Occasionally, epidemics flare when a balance is upset, but in stable host populations, even occasional epidemics are not extremely serious.

Generally, host-specific parasites retain a great deal of specificity when transplanted to the Islands and therefore pose little threat to potential new hosts. Even though their introduction to Hawai'i results in a superficial "exposure" to new avian groups, most parasite distributions are inhibited by less obvious factors, including the lack of potential vectors and intermediate hosts, eating habits of potential hosts, and humidity and soil conditions that affect survival of ova. If these factors are overcome, when confronted with the physiology of a new host, the final destination of the parasite within the host tissue may be abberrant, or as is the case of the acanthocephalan Mediorhynchus orientalis, larvae may fail to reach sexual maturity.

Those parasites that readily cross species boundaries, infecting a diverse spectrum of hosts, cause diseases with which managers and biologists in Hawai'i need to be most concerned, because it is these that have the greatest ability to impact native birds. However, not all cause severe diseases. The most widespread parasite reported in the widest variety of Hawaiian species is the eyeworm, Oxyspirura mansoni, which typically causes little harm to its host populations. Its distribution is probably limited only by the intermediate host. If a means of transmission is available when a non-specific disease arrives (e.g., proper vector), native and introduced birds become immediate new targets. Unfortunately, because the native birds are often "naive" in the evolutionary sense, they tend to be more susceptible than are introduced species--as in the well-studied case of avian malaria.

Avian malaria is a parasitic infection of the blood, caused in Hawai'i by the protozoan Plasmodium relictum. It infects a wide range of avian species, has probably contributed to the extinction of some native bird species, and certainly contributes to limited distributions of others. Malaria was reported as early as 1947 by Fisher and Baldwin, but the case against Plasmodium crystallized with Warner (1968), although he failed to find any native birds infected in the wild. He did, however, show a high degree of susceptibility to the malarial parasite by native birds when exposed experimentally. He proposed that malaria had greatly influenced bird distribution and was a major factor in their demise.

Of all the diseases and parasites recorded from the native Hawaiian avifauna, malaria has been the best studied ecologically and appears to be presently having the greatest influence on these birds. During the course of an extensive field and laboratory study, van Riper et al. (in press) found that on Hawai'i Island native birds had a high incidence of infection in their populations, and more severe infections, than did the introduced species. Elevation and climate relating to the vector's distribution seemed to be related to infection levels and were strongly reflective of species distribution. Van Riper et al. (in press) suggested that malaria is one of the major bird population-regulating mechanisms operative on Hawai'i Island today, and appears to be restricting the native Hawaiian land birds to the higher and drier forest areas.

Another widespread disease capable of readily infecting a variety of bird species is avian pox. Lesions typical of avian pox have been mentioned for many years since Perkins (1893, 1903), who first described open sores on several native species. Since avian pox has probably been in the Islands for almost 100 years, surviving bird species appear to have adapted a degree of resistance. Field workers continue to observe a high incidence of lesions and evidence of past lesions (e.g., missing toes), and a thorough study of birds that have a history of lesions would perhaps be enlightening. Avian pox probably led to the deaths of countless Hawaiian birds, and even entire species, early in the century, but there are few data to support this. Of first priority in the study of Hawaiian bird diseases should be a complete study of avian pox, examining geographic distribution, host infection rates, and susceptibility of various avian species. The investigation should contain laboratory work complimented by field surveys. Avian pox has long been enigmatic in Hawaiian disease studies and probably is more important than has been believed.

Other non-host specific diseases may be shown to be important to Hawaiian birds, and more study is needed in this area. A paucity of data exists in Hawai'i concerning bacterial and viral diseases in general. Moreover, all diseases and parasites should be examined in terms of ecosystem and island type. Areas of disease concentration should be mapped throughout the Islands; possibly the absence of birds in particular ecosystems might be thus explained. With more information, controlling diseases might become more feasible.

At present it is important that no new diseases be introduced to the Islands. The obvious solution is a more careful control in the importation of avian species, including the monitoring and clearing of all parasites in imported birds. The Hawaiian goose and other captive-bred species should be carefully examined for disease before being introduced into wild populations. For example, Avery (1966) reported a gapeworm (Cyathosthoma sp.), mycrobacteriosis, and 2 species of tapeworms (Menatoparataiena southwelli and Fimbiaria fasiolaris) from captive Hawaiian geese at Slimbridge, England. It is not known if any of these are yet in Hawai'i, but great care should be taken to prevent their introduction. There is evidence that arboviruses, Newcastle disease, and avian influenza similarly are absent (Quisenberry and Wallace 1959; Wallace et al. 1964; U.S. Department of Agriculture and Southeastern Cooperative Wildlife Disease Study 1980; Okimoto 1975), and they should be carefully guarded against.

In summary, we understand some of the impacts that diseases have had on Hawaiian birds. However, more information is needed for long-term predictions regarding the well-being of this unique compliment of avian species. And, while parasites and diseases are only a few of the many threats that confront the continued existence of Hawai'i's birds, they need to be fully considered in any program of management and preservation.

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APPENDIX

Parasite and Disease Records of Hawaiian Birds[1]

Procellariiformes

Black-footed albatross   *Diomedea nigripes*

Acari
- *Leptotrombidium intermedium* (nest) - Goff 1971
- *Neoschoengastia gallinarum* (nest) - Goff 1971
- *Neotrombicula tamiayi* (nest) - Goff 1971
- *Ornithodoros capensis* (nest) - Wilson 1964a

Mallophaga
- *Harrisoniella* sp. - Thompson 1948

Hippoboscidae
- *Olfersia aenescens* - Maa 1968

Laysan albatross   *Diomedea immutabilis*

Acari
- *Ixodes laysanensis* - Wilson 1964a
- *Neoschoengastia gettmanni* (nest) - Goff 1984
- *Ornithodoros capensis* (nest) - Kohls, Sonenshine, and Clifford 1965; Wilson 1964a

Mallophaga
- *Docophoroides* sp. - Thompson 1948
- *Harrisoniella* sp. - Thompson 1948

Hippoboscidae
- *Olfersia aenescens* - Maa 1968

Wedge-tailed shearwater   *Puffinus pacificus*

Acari
- *Ixodes laysanensis* - Wilson 1964a
- *Ornithodoros capensis* - Takahashi et al. 1982

Mallophaga
- *Halipeurus mirabilis* - Thompson 1948
- *Longimenopon puffinus* - Thompson 1948
- *Trabeculus mirabilis* - Thompson 1948

Hippoboscidae
- *Olfersia aenescens* - Bequaert 1941

Christmas shearwater   *Puffinus nativitatus*

Mallophaga
- *Longimenopon puffinus* - Thompson 1948

Townsend's (Newell's) shearwater   *Puffinus auricularis*

Protozoa
- *Plasmodium* sp. - Warner 1968 in dark-rumped petrel; corrected by Banko 1980

Acari
- *Ornithodoros capensis* (nest) - Wilson 1964a

Red-footed booby   *Sula sula*

Hippoboscidae
- *Olfersia aenescens* - Maa 1968

Pelecaniformes

Red-tailed tropicbird *Phaethon rubricauda*
Viruses
Avian pox - Locke, Wirtz, and Brown 1965

Great frigatebird *Fregata minor*
Acari
Neottialges fregatae - Fain and Amerson 1968
Neottialges hawaiiensis - Fain and Amerson 1968
Hippoboscidae
Olfersia spinifera - Bequaert 1941; Maa 1968

Ciconiiformes

Cattle egret *Bulbulcus ibis*
Trematoda
Philophthalmus gralli - Alicata 1969

Black-crowned night heron *Nycticorax nycticorax*
Acari
Opthalmognathus tenorioae - Fain and Goff 1980
Trematoda
Centrocestus formosanus - Martin 1958
Haplorchis taichui - Martin 1958
Haplorchis yokogawai - Martin 1958
Bacteria
Botulism - Brock and Breese 1953

Anseriformes

Hawaiian goose (nene) *Nesochen sandvicensis*
Nematoda
Amidostomum sp. - Banko and Manuwal 1982
Heterakis sp. - Banko and Manuwal 1982

Green-winged teal *Anas crecca*
Bacteria
Botulism - Brock and Breese 1953

Hawaiian duck *Anas wyvilliana*
Cestoda
Hymenolepis megalops - Alicata 1964
Mallophaga
Anaticola crassicorne - Schwartz and Schwartz 1953
Trinotin querquedulae - Schwartz and Schwarts 1953

Laysan duck (teal) — *Anas laysanensis*

Acari

Ixodes laysanensis (in ear) - Butler 1961; Butler and Usinger 1963

Northern pintail — *Anas acuta*

Bacteria

Botulism - Brock and Breese 1953

Northern shoveler — *Anas clypeata*

Bacteria

Botulism - Brock and Breese 1953

American wigeon — *Anas americana*

Bacteria

Botulism - Brock and Breese 1953

Greater scaup — *Aythya marila*

Bacteria

Botulism - Brock and Breese 1953

Bufflehead — *Bucephala albeola*

Bacteria

Botulism - Brock and Breese 1953

Galliformes

Gray francolin — *Francolinus pondicerianus*

Nematoda

Heterakis gallinarum - Lewin and Holmes 1971

Oxyspirura mansoni - Lewin and Holmes 1971

Subulura brumpti - Lewin and Holmes 1971

Bare-throated francolin — *Pternistes leucoscepus*

Nematoda

Oxyspirura sp. - Lewin and Holmes 1971

Oxyspirura mansoni - Lewin and Holmes 1971

Barbary partridge — *Alectoris barbara*

Nematoda

Dispharynx nasuta - Lewin and Holmes 1971

Oxyspirura mansoni - Lewin and Holmes 1971

Cestoda

Choanotaenia infundibulum - Lewin and Holmes 1971

Japanese quail — *Coturnix japonica*

Nematoda

Oxyspirura mansoni - Schwartz and Schwartz 1949, 1951

Subulura sp. - Schwartz and Schwartz 1949

Subulura brumpti - Lewin and Holmes 1971; Schwartz and Schwartz 1951

Cestoda
Choanotaenia infundibulum - Lewin and Holmes 1971
Acari
Xoloptes sp. - Schwartz and Schwartz 1949
Mallophaga
Goniocotes asterocephalus - Schwartz and Schwartz 1949
Hippoboscidae
Ornithoica vicina - Schwartz and Schwartz 1949, 1951

Kalij pheasant *Lophura leucomelana*
Nematoda
Oxyspirura mansoni - Lewin and Mahrt 1983
Mallophaga
Amyrsidea monostoecha - Lewin and Mahrt 1983
Lagopoecus colchicus - Lewin and Mahrt 1983

Red junglefowl *Gallus gallus*
Mallophaga
Goniodes sp. (larvae) - Schwartz and Schwartz 1949
Goniodes dissimilis - Schwartz and Schwartz 1949
Lipeurus caponis - Schwartz and Schwartz 1949, 1951
Menopon gallinae - Schwartz and Schwartz 1949
Hippoboscidae
Ornithoica vicina - Schwartz and Schwartz 1949, 1951

Domestic chicken *Gallus gallus*
Protozoa
Eimeria tenella - Alicata 1947, 1964
Histomonas meleagridis - Alicata 1964
Nematoda
Ascaridia galli - Alicata 1964; Swanson 1939
Ascaridia perspicillum - Guberlet 1926
Cheilospirura hamulosa - Alicata 1938b; Swanson 1939
Dispharynx nasuta - Alicata 1964; (= *D. spiralis*) Swanson 1939
Gongylonemum ingluvicola - Alicata 1964
Heterakis sp. - Swanson 1939
Heterakis gallinarum - Alicata 1964; Guberlet 1926
Oxyspirura mansoni - Alicata 1936; Schwabe 1950, 1951; Swanson 1939
Subulura sp. - Swanson 1939
Subulura brumpti - Alicata 1939b
Tetrameres americana - Alicata 1964; Swanson 1939

Cestoda
- *Choanotaenia infundibulum* - Alicata 1938a; Guberlet 1926
- *Hymenolepis carioca* - Alicata 1938a; Guberlet 1926
- *Orientolepis exigua* - Alicata 1938a
- *Raillietina cesticillus* - Alicata 1938a; Guberlet 1926
- *Raillietina tetragona* - Alicata 1938a; Guberlet 1926

Trematoda
- *Philophthalmus gralli* (experimental infection) - Alicata 1962; Alicata and Noda 1960; Ching 1961
- *Postharmostomum gallinum* - Alicata 1940

Acari
- *Cytodites nudus* (air passage, liver, lungs) - Bice 1932
- *Dermanyssus gallinae* - Alicata et al. 1946; Pemberton 1943
- *Knemidokoptes mutans* (leg) - Bice 1932
- *Megninia cubitalis* - Alicata et al. 1946
- *Mesoknemidocoptes laevis* (leg) - Bice 1932
- *Ornithonyssus bursa* - Zimmerman 1944
- *Ornithonyssus sylviarum* (feather) - Garrett and Haramoto 1967
- *Pterolichus obtusus* - Alicata et al. 1946

Mallophaga
- *Chelopistes meleagridis* - Illingsworth 1928
- *Cuclotogaster heterographa* - Illingsworth 1928
- *Goniocotes gallinae* - Illingsworth 1928
- *Goniodes dissimilis* - Zimmerman 1948
- *Goniodes gigas* - Illingsworth 1928
- *Lipeurus caponis* - Illingsworth 1928
- *Menacanthus stramineus* - Illingsworth 1928
- *Menopon gallinae* - Illingsworth 1928

Siphonaptera
- *Echidnophaga gallinacea* - Illingsworth 1916; Pemberton 1943

Ring-necked pheasant *Phasianus colchichus*

Nematoda
- *Ascaridia* sp. - (probably *A. galli*) Schwartz and Schwartz 1949, 1951
- *Cheilospirura* sp. - Schwartz and Schwartz 1949
- *Cheilospirura hamulosa* - Schwartz and Schwartz 1951
- *Cyrnea graphophasiani* - Schwartz and Schwartz 1951
- *Gongylonemum ingluvicola* - Swanson 1939
- *Heterakis* sp. - Schwartz and Schwartz 1949
- *Heterakis gallinarum* - Lewin and Holmes 1971; Schwartz and Schwartz 1951

Oxyspirura mansoni - Alicata 1936; Lewin and Holmes 1971; Schwartz and Schwartz 1949, 1951; Schwabe 1950, 1951; Swanson 1939
Subulura sp. - Schwartz and Schwartz 1949
Subulura brumpti - Lewin and Holmes 1971; Schwartz and Schwartz 1951
Trematoda
Philophthalmus gralli - Lewin and Holmes 1971
Acari
Megninia columbae - Schwartz and Schwartz 1949, 1951
Megninia ginglymura - Schwartz and Schwartz 1949, 1951
Mallophaga
Goniocotes hologaster - Zimmerman 1948
Goniodes sp. (larvae) - Schwartz and Schwartz 1949, 1951
Goniodes colchici - Schwartz and Schwartz 1949, 1951
Goniodes mammillatus (= G. mammilatus) - Schwartz and Schwartz 1949, 1951
Lipeurus caponis - Schwartz and Schwartz 1949, 1951; Zimmerman 1948
Lipeurus maculosus - Schwartz and Schwartz 1949, 1951
Menopon fulvomaculatum - Schwartz and Schwartz 1949, 1951
Uchida sp. - Schwartz and Schwartz 1949, 1951
Hippoboscidae
Ornithoica vicina - Bequaert 1941; Maa 1966; Schwartz and Schwartz 1949, 1951

Common peafowl — Pavo cristatus
Mallophaga
Menopon phaeostomum - Illingsworth 1928

Wild turkey — Meleagris gallopavo
Nematoda
Oxyspirura mansoni - Lewin and Holmes 1971
Subulura brumpti - Lewin and Holmes 1971
Cestoda
Metroliasthes lucida - Lewin and Holmes 1971
Orientolepis exigua - Lewin and Holmes 1971

Domestic turkey — Meleagris gallopavo
Protozoa
Histomonas meleagridis - Alicata 1947, 1964
Nematoda
Cheilospirura hamulosa - Alicata 1964
Dispharynx nasuta - Alicata 1964
Heterakis gallinarum - Alicata 1964
Mallophaga
Chelopistes meleagridis - Illingsworth 1928
Goniocotes gallinae - Illingsworth 1928

Menopon gallinae - Illingsworth 1928
Oxylipeurus polytrapezius - Illingsworth 1928

California quail — *Callipepla californica*
Nematoda
Aulonocephalus pennula - Lewin and Holmes 1971
Dispharynx nasuta - Lewin and Holmes 1971
Oxyspirura sp. - Lewin and Holmes 1971
Oxyspirura mansoni - Lewin and Holmes 1971
Subulura brumpti - Lewin and Holmes 1971
Cestoda
Fuhrmannetta crassula - Lewin and Holmes 1971
Choanotaenia infundibulum - Lewin and Holmes 1971
Acari
Xoloptes sp. - Schwartz and Schwartz 1949
Mallophaga
Goniodes sp. (larvae) - Schwartz and Schwartz 1949
Goniodes mammillatus - Schwartz and Schwartz 1949; Zimmerman 1948
Lagopoecus docophoroides - Schwartz and Schwartz 1949
Menopon sp. - Schwartz and Schwartz 1949
Menopon fulvomaculatum - Schwartz and Schwartz 1949
Siphonaptera
Echidnophaga gallinacea - Schwartz and Schwartz 1949, 1951

Helmeted guineafowl — *Numida meleagris*
Mallophaga
Goniodes gigas - Zimmerman 1948
Menopon gallinae - Illingsworth 1928
Menopon phaeostomum - Illingsworth 1928

Gruiformes

American coot — *Fulica americana*
Trematoda
Philophthalmus gralli - Alicata 1969
Mallophaga
Quadraceps oraria - Zimmerman 1948
Rallicola advena - Zimmerman 1948
Bacteria
Botulism - Brock and Breese 1953

Charadriiformes

Lesser golden plover — *Pluvialis dominica*
Nematoda
Porrocaecum ensicaudatum - Okimoto 1975
Porrocaecum semiteres - Okimoto 1975

Subulura skrjabinensis - Okimoto 1975
Acanthocephala
Mediorhynchus sp. (probably *M. orientalis*) - Smith and Guest 1974
Mediorhynchus orientalis - Okimoto 1975; Schmidt and Kuntz 1977
Plagiorhynchus charadrii - Okimoto 1975; Smith and Guest 1974
Acari
Neoschoengastia gallinarum (nest) - Goff 1971
Rhinonyssus coniventris - Wilson 1964b
Toritrombicula oahuensis - Goff 1977
Mallophaga
Colpocephalum brachysomum - Zimmerman 1948
Quadraceps birostris - Zimmerman 1948
Saemundssonia conicus - Zimmerman 1948

Black-necked stilt *Himantopus mexicanus*
Bacteria
Botulism - Brock and Breese 1953

Wandering tattler *Heteroscelus incanus*
Mallophaga
Actornithophilus kilauensis - Zimmerman 1948

Saemundssonia conicus - Zimmerman 1948

Bristle-thighed curlew *Numenius tahitiensis*
Mallophaga
Lunaceps sp. - Thompson 1948

Red-necked phalarope *Phalaropus lobatus*
Mallophaga
Quadraceps connexa - Thompson 1948

Ruddy Turnstone *Arenaria interpres*
Trematoda
Austrobilharzia variglandis - Chu and Cutress 1954
Acari
Guntherana domrowi - Brennan 1965; Goff 1984
Ixodes laysanensis - Wilson 1964a

Glaucous gull *Larus hyperboreus*
Mallophaga
Austromenopon infrequens - Thompson 1948

Gray-backed tern *Sterna lunata*
Mallophaga
Quadraceps birostris - Zimmerman 1948
Saemundssonia snyderi - Thompson 1948; Zimmerman 1948

Sooty tern — *Sterna fuscata*
- Acari
  - *Ornithodoros capensis* - Amerson 1966
- Mallophaga
  - *Saemundssonia snyderi* - Thompson 1948
- Hippoboscidae
  - *Olfersia aenescens* - Maa 1968

Brown noddy — *Anous stolidus*
- Acari
  - *Guntherana domrowi* - Brennan 1965; Goff 1984
  - *Ornithodoros capensis* - Kohls, Sonenshine, and Clifford 1965
  - *Ornithodoros denmarki* - Kohls, Sonenshine, and Clifford 1965
- Mallophaga
  - *Actornithophilus epiphanes* - Zimmerman 1948
  - *Actornithophilus milleri* - Thompson 1948
  - *Austromenopon sternophilum* - Thompson 1948
  - *Colpocephalum discrepans* - Zimmerman 1948
  - *Quadraceps separata* - Thompson 1948; Zimmerman 1948

Columbiformes

Rock dove (pigeon) — *Columba livia*
- Protozoa
  - *Haemoproteus columbae* - Alicata 1947, 1964; Kartman 1949; Navvab Gojrati 1970; Yeager and Gleiser 1946; van Riper[2]
  - *Plasmodium* sp. (probably *P. relictum*) - Navvab Gojrati 1970
  - *Plasmodium relictum* - van Riper[2]
  - *Trichomonas gallinae* - Yeager and Gleiser 1946
- Nematoda
  - *Ascaridia* sp. - Schwartz and Schwartz 1949
  - *Dispharnyx nasuta* - Alicata 1964
  - *Ornithostrongylus quadriradiatus* - Alicata 1939a
  - *Tetrameres* sp. - van Riper[2]
  - *Oxyspirura mansoni* - van Riper[2]
- Cestoda
  - *Raillietina* sp. - Yeager and Gleiser 1946
- Acari
  - *Falculifer rostratus* - Yeager and Gleiser 1946
  - *Gabucinia* sp. - Garrett and Haramoto 1967
  - *Megninia columbae* - Schwartz and Schwartz 1949
- Mallophaga
  - *Columbicola columbae* - Schwartz and Schwartz 1949; Yeager and Gleiser 1946; Zimmerman 1944, 1948
  - *Colpocephalum turbinatum* - Zimmerman 1948
  - *Goniocotes bidentatus* - Schwartz and Schwartz 1949
  - *Menopon gallinae* - Illingsworth 1928

Hippoboscidae
Ornithoica vicina - Maa 1966
Pseudolynchia canariensis - Bequaert 1941; Bryan 1934; Schwartz and Schwartz 1949, 1959; Yeager and Gleiser 1946

Spotted dove (Chinese, Lace-necked dove) Streptopelia chinensis
Nematoda
Ascaridia sp. - Schwartz and Schwartz 1949
Oxyspirura mansoni - Alicata 1947; Schwartz and Schwartz 1949, 1951; Smith and Guest 1974
Subulura brumpti - Schwartz and Schwartz 1951
Acari
Pterolichus sp. - Alicata, Kartman, and Fisher 1948
Mallophaga
Columbicola sp. - Schwartz and Schwartz 1949
Columbicola columbae - Zimmerman 1948
Goniocotes chinensis - Schwartz and Schwartz 1949; Zimmerman 1948
Goniodes sp. (larvae) - Schwartz and Schwartz 1949
Goniodes lativentris - Zimmerman 1948 ("Dove" = probably this bird)
Myrsidea invadens - Zimmerman 1948 ("Dove" = probably this bird)

Zebra dove (Barred dove) Geopelia striata
Protozoa
Trichomonas gallinae - Kocan and Banko 1974
Nematoda
Dispharnyx sp. - van Riper[2]
Oxyspirura mansoni - Smith and Guest 1974
Acari
Mesonyssus geopeliae - Wilson 1966
Ornithonyssus bursa - Alicata, Kartman, and Fisher 1948
Mallophaga
Columbicola sp. - Schwartz and Schwartz 1949
Columbicola columbae - Alicata, Kartman, and Fisher 1948; Zimmerman 1948
Goniodes sp. - Alicata, Kartman, and Fisher 1948
Goniocotes asterocephalus - Schwartz and Schwartz 1949
Goniocotes chinensis - Schwartz and Schwartz 1949; Zimmerman 1948
Menopon sp. (larvae) - Schwartz and Schwartz 1949

Strigiformes

Common barn owl — *Tyto alba*

- Hippoboscidae
  - *Ornithoica vicina* - Maa 1969a

Short-eared owl (Pueo, Hawaiian owl) — *Asio flammeus*

- Acari
  - Xolalgidae n.gen., n.sp. (body wash) - Goff 1980
- Mallophaga
  - *Colpocephalum brachysomum* - Zimmerman 1948
- Hippoboscidae
  - *Icosta nigra* - Bequaert 1941
  - *Ornithoica vicina* - Bequaert 1941; Maa 1966
- Fungi
  - *Aspergillus fumigatus* (captive) - Honolulu Zoo Necropsy Reports 1967

Passeriformes

Hawaiian crow ('Alala) — *Corvus hawaiiensis*

- Protozoa
  - *Plasmodium relictum* - Jenkins and van Riper, in prep.
- Acari
  - *Analges* sp. - M.L. Goff, pers. comm.
  - *Gabucinia delibatus* - M.L. Goff, pers. comm.
  - *Mesalgoides* sp. - M.L. Goff, pers. comm.
  - *Ornithonyssus bursa* (nest) - Garrett and Haramoto 1967; Tomich 1967
  - *Ornithonyssus sylviarum* - Banko 1974

Millerbird — *Acrocephalus familiaris*

- Acari
  - *Pterodectes* sp. - M.L. Goff, pers. comm.
  - *Pteroherpus oxyplax* - M.L. Goff, pers. comm.
  - *Trouessartia trouessarti* - M.L. Goff, pers. comm.
  - Xolalgidae n.gen., n.sp. - M.L. Goff, pers. comm.

'Elepaio — *Chasiempsis sandwichensis*

- Protozoa
  - *Isopora* sp. - van Riper[2]
  - *Plasmodium relictum* - van Riper et al., in press
- Acari
  - *Ornithonyssus sylviarum* (nest) - Goff 1980
- Viruses
  - Avian pox - van Riper[2]
- Bacteria
  - *Streptococcus* - van Riper[2]

White-rumped shama — *Copsychus malabaricus*

Acari

Bakericheyla chanayi - Radovsky 1971

Hawaiian thrush — *Phaeornis obscurus*

Protozoa

Isospora phaeornis - Levine, van Riper, and van Riper 1980

Plasmodium relictum - van Riper et al., in press

Acari

Analges sp. (body wash) - Goff 1980

Proctophyllodes sp. (body wash) - Goff 1980

Pterodectes sp. (body wash) - Goff 1980

Ptilonyssus sp. (body wash) - Goff 1980

Trouessartia sp. (body wash) - Goff 1980

Viruses

Avian pox - van Riper[2]

Fungi

Aspergillus fumigatus - van Riper[2]

Red-billed leiothrix — *Leiothrix lutea*

Protozoa

Plasmodium sp. (probably *P. relictum*) - Baldwin 1941

Plasmodium relictum - van Riper et al., in press

Plasmodium vaughani (probably *P. relictum*) - Fisher and Baldwin 1947

Acari

Cytodites nudas (body wash) - Goff 1980; M.L. Goff, pers. comm.

Neocheyletiella media (body wash) - Goff 1980

Ornithocheyletia leiothrix (body wash) - Goff 1980; M.L. Goff, pers. comm.

Pteronyssidae n.gen., n.sp. (body wash) - Goff 1980

Common myna — *Acrodotheres tristis*

Protozoa

Plasmodium relictum - van Riper[2]

Nematoda

Dispharnyx sp. - Smith and Guest 1974

Microtetrameres sp. - Alicata, Kartman, and Fisher 1948; Smith and Guest 1974

Oxyspirura mansoni - Alicata 1947, 1964; Eddinger 1967; Swanson 1939

Acanthocephala

Mediorhynchus sp. (Probably *M. orientalis*) - Smith and Guest 1974

Acari

Montesauria sp. - Alicata, Kartman, and Fisher 1948

Ornithonyssus bursa - Berger 1981; Zimmerman 1944

Pteronyssus sp. - Alicata, Kartman, and Fisher 1948
Trouessartia sp. - Alicata, Kartman, and Fisher 1948
Mallophaga
Menacanthus spinosus - Alicata, Kartman, and Fisher 1948
Myrsidea invadens - Alicata, Kartman, and Fisher 1948

Japanese white-eye *Zosterops japonicus*
Protozoa
Isospora bravi - Levine, van Riper, and van Riper 1980
Plasmodium sp. (probably *P. relictum*) - Baldwin 1941
Plasmodium relictum - van Riper et al., in press
Nematoda
Microtetrameres sp. - Smith and Guest 1974
Procyrnea longialatus - Cid del Prado Vera, Maggenti, and van Riper, in press
Synhimantus zosteropsi - Cid del Prado Vera, Maggenti, and van Riper, in press
Acari
Anhemialges sp. (body wash) - Goff 1980
Calcealges yunkeri (body wash) - Goff 1980
Dermoglyphus elongatus - Alicata, Kartman, and Fisher 1948
Megninia sp. - Alicata, Kartman, and Fisher 1948
Mouchetia sp. (body wash) - Goff 1980
Pteronyssus sp. - Alicata, Kartman, and Fisher 1948
Ptilonyssus sp. (nasal cavity) - Smith and Guest 1974
Ornithocheyla sp. (body wash) - Goff 1980
Ornithonyssus sylviarum (nest) - Goff 1980
Strelkovarius sp. (body wash) - Goff 1980
Trouessartia sp. - Alicata, Kartman, and Fisher 1948; Goff 1980
Hippoboscidae
Ornithoica vicina - Hardy 1952
Viruses
Avian pox - van Riper[2]

Red-crested cardinal *Paroaria coronata*
Nematoda
Dispharnyx sp. - Smith and Guest 1974
Oxyspirura mansoni - Berger 1981; Smith and Guest 1974
Syngamus trachea - Smith 1973b
Tetrameres sp. - Smith and Guest 1974

Acanthocephala
Mediorhynchus sp. (probably M. orientalis) - Smith and Guest 1974
Acari
Ptilonyssus sp. (nasal cavity) - Smith and Guest 1974
Mallophaga
Myrsidea incerta - Alicata, Kartman, and Fisher 1948

Northern cardinal *Cardinalis cardinalis*
Protozoa
Isospora vanriperorum - Levine, van Riper, and van Riper 1980
Plasmodium relictum - van Riper et al., in press
Nematoda
Capillaria sp. - Smith and Guest 1974
Dispharnyx sp. - Smith and Guest 1974
Acanthocephala
Mediorhynchus sp. (probably M. orientalis) - Smith and Guest 1974
Acari
Proctophyllodes longiphyllus - Garrett and Haramoto 1967
Viruses
Avian pox - van Riper[2]

House finch *Carpodacus mexicanus*
Protozoa
Atoxoplasma sp. - van Riper[2]
Plasmodium relictum - van Riper et al., in press
Plasmodium sp. (probably P. relictum) - Warner 1968
Nematoda
Syngamus trachea - Smith and Guest 1974
Acari
Ornithonyssus sylviarum (body wash) - Goff 1980
Proctophyllodes pinnatus (body wash) - Goff 1980
Proctophyllodes vegetans - Garrett and Haramoto 1967
Mallophaga
Colpocephalum discrepans - Zimmerman 1948
Philopterus subflavescens - Zimmerman 1948
Viruses
Avian pox - van Riper[2]
Bacteria
Escherichia coli (captive) - van Riper[2]

Laysan finch *Telespyza cantans*
Acari

Schoengastia pobsa - Brennan and Amerson 1971; Goff 1984

Viruses

Avian pox (captive) - van Riper[2]

Bacteria

Staphylococcus epidermis (captive) - van Riper[2]

Streptococcus (captive) - van Riper[2]

Pseudomonas aeruginosa (captive) - van Riper[2]

Klebsiella pneumoniae (captive) - van Riper[2]

Serratia marcescens (captive) - van Riper[2]

Citrobacter diversus (captive) - van Riper[2]

Fungi

Candida albicans (captive) - van Riper[2]

Nihoa finch — Telespyza ultima

Acari

Analges sp. - M.L. Goff, pers. comm.

Boydaia agelaii - M.L. Goff, pers. comm.

Eutrombicula conantae - Goff 1984

Ingrassiella sp. - M.L. Goff, pers. comm.

Neoschoengastia ewingi - Goff 1984

Proctophyllodes sp. - M.L. Goff, pers. comm.

Toritrombicula nihoaensis - Goff 1984

Palila — Loxioides bailleui

Bacteria

Salmonella - van Riper[2]

Common 'amakihi — Hemignathus virens

Protozoa

Isospora loxopis - Levine, van Riper, and van Riper 1980

Plasmodium relictum - van Riper 1975; van Riper et al., in press

Nematoda

Viguiera hawaiiensis - Cid del Prado Vera, Maggenti, and van Riper, in press

Cestoda

Anonchotaenia brasilense - Vogue and Davis 1953; van Riper[2]

Trematoda

Urotocus rossittensis - van Riper[2]

Acari

Analges sp. - Goff 1980

Cheyletus malaccensis - Goff 1980; M.L. Goff, pers. comm.

Harpyrhynchus sp. - Goff 1980

Ornithonyssus sp. - Berger 1981

Ornithonyssus sylviarum (nest) - Goff 1980

Proctophyllodes sp. - Goff 1980

Pterodectes sp. - Goff 1980

Ptilonyssus sp. (nasal cavity) - Goff 1980

Rhinonyssus sp. (nasal cavity)
- van Riper 1975
Trouessartia sp. - Goff 1980
Mallophaga
Machaerilaemus hawaiiensis - Zimmerman 1948
Philopterus macgregori - Zimmerman 1948
Hippoboscidae
Ornithoica vicina - Bequaert 1941; Maa 1966
Viruses
Avian pox - van Riper[2]
Fungi
Aspergillus fumigatus (captive)
- Honolulu Zoo Necropsy Reports 1966

'Anianiau *Hemignathus parvus*
Protozoa
Isopora sp. (captive) - van Riper 1975
Acari
Megnina sp. - Haramoto in Berger 1981

Kaua'i 'akialoa *Hemignathus procerus*
Acanthocephala
Apororhynchus hemignathi - Perkins 1903
Cestoda
Drepanidotaenia hemignathi - Perkins 1903

'Akepa *Loxops coccineus*
Viruses
Avian pox - Henshaw 1902

'I'iwi *Vestiaria coccinea*
Protozoa
Plasmodium relictum - van Riper et al., in press
Nematoda
Viguiera hawaiiensis - Cid del Prado Vera, Maggenti, and van Riper, in press
Cestoda
Anonchotaenia brasilense - Vogue and Davis 1953; van Riper[2]
Acari
Analges sp. - Goff 1980
Cheyletus eruditus - Goff 1980; M.L. Goff, pers. comm.
Cheyletus sp. - Berger 1981
Ingressiella sp. - Goff 1980
Proctophyllodes sp. - Goff 1980
Mallophaga
Colpocephalum hilensis - Zimmerman 1948
Myrsidea cyrtostigma - Alicata 1969; Zimmerman 1948
Hippoboscidae
Ornithoica vicina - Bequaert 1941; Maa 1966
Viruses
Avian pox - van Riper[2]

Bacteria

Staphylococcus epidermis - van Riper[2]

Citrobacter fruendii - van Riper[2]

'Apapane — *Himatione sanguinea*

Protozoa

Plasmodium relictum - Navvab Gojrati 1970; van Riper et al., in press

Trichomonas gallinae - van Riper[2]

Nematoda

Procyrnea longialatus - Cid del Prado Vera, Maggenti, and van Riper, in press

Viguiera hawaiiensis - Cid del Prado Vera, Maggenti, and van Riper, in press

Cestoda

Anonchotaenia brasilense - Vogue and Davis 1953; van Riper[2]

Trematoda

Urotocus rossittensis - van Riper[2]

Acari

Analges sp. - Goff 1980

Androlaelaps sp. - Goff 1980

Anhemialges sp. - Goff 1980

Calcealges sp. - Goff 1980

Harpyrhynchus sp. - Goff 1980

Mouchetia sp. - Goff 1980

Proctophyllodes sp. - Goff 1980

Pterodectes sp. - Goff 1980

Ptilonyssus sp. (2 new species) (nasal cavity) - Goff 1980

Mallophaga

Myrsidea cyrtostigma - Zimmerman 1948

Viruses

Avian pox - van Riper[2]

Bacteria

Klebsiella pneumoniae - van Riper[2]

Escherichia coli - van Riper[2]

Pseudomonas pseudoalcaligens - van Riper[2]

Enterobacter cloacae - van Riper[2]

Fungi

Candida albicans (captive) - A. Miyahara, pers. comm.

House sparrow — *Passer domesticus*

Protozoa

Atoxoplasma sp. - van Riper et al., in press

Plasmodium relictum - van Riper et al., in press

Nematoda

Oxyspirura mansoni - Illingsworth 1931

Tetrameres sp. - Kartman 1951

Acari

Boydaia nigra - Fain and Goff 1980

Dermatophagoides evansi (body wash) - Goff 1980; M.L. Goff, pers. comm.

Haemolaelaps fenilis - Alicata, Kartman, and Fisher 1948
Harpyrhynchus pilirostris - Garrett and Haramoto 1967; Goff 1980
Neonyssus sp. - Alicata, Kartman, and Fisher 1948
Ornithonyssus bursa (nest) - Garrett and Haramoto 1967; Zimmerman 1944
Ornithonyssus sylviarum (nest) - Goff 1980
Proctophyllodes truncatus - Alicata, Kartman, and Fisher 1948
Ptilonyssus hirsti - Wilson 1964b; Goff 1980

Mallophaga
Bruelia vulgata - Zimmerman 1948
Myrsidea sp. - Alicata, Kartman, and Fisher 1948

Hippoboscidae
Ornithoica vicina - Alicata, Kartman, and Fisher 1948; Maa 1966

Viruses
Avian pox - van Riper[2]

Blue-capped cordonbleu   Uraeginthus cyanocephala

Nematoda
Capillaria sp. - Smith and Guest 1974

Acari
Sternostoma tracheacolum (respiratory tract) - Smith and Guest 1974; (internal organs) Smith 1973a

Lavender waxbill   Estrilda caerulescens

Nematoda
Tetrameres sp. - Smith and Guest 1974

Acari
Ptilonyssus sp. (nasal cavity) - Smith and Guest 1974

Orange-cheeked waxbill   Estrilda melpoda

Nematoda
Capillaria sp. - Smith and Guest 1974

Acari
Sternostoma tracheacolum (body cavity) - Smith and Guest 1974

Black-rumped waxbill (Red-eared)   Estrilda troglodytes

Acari
Sternostoma tracheacolum (internal organs) - Smith 1973a

Nutmeg mannikin (Ricebird)   Lonchura punctulata

Protozoa
Atoxoplasma sp. - van Riper et al., in press

Isospora ivensae - Levine, van Riper, and van Riper 1980
Plasmodium relictum - van Riper et al., in press
Trichomonas gallinae (captive) - Smith and Guest 1974

Acari
Haemolaeplaps fenilis (nest) - Garrett and Haramoto 1967
Onychalges sp. - Goff 1980
Paraneonyssus sp. (nasal cavity) - Goff 1980
Pterodectes sp. - Goff 1980
Ptilonyssus sp. (nasal cavity) - Goff 1980
Trouessartia sp. - Goff 1980

Mallophaga
Bruelia stenzona - Zimmerman 1948
Philopterus subflavescens - Zimmerman 1948

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[1] Taxonomy of the avian species follows the A.O.U. Check-list of North American Birds 1983.

[2] Parasites and diseases found by the authors but not previously published.

LITERATURE CITED

Alicata, J.E. 1936. Poultry parasites. Hawaii Agric. Exp. Stn. Rep. 1936, 79-82.

Alicata, J.E. 1938a. Studies on poultry parasites. Hawaii Agric. Exp. Stn. Rep. 1937, 93-96.

Alicata, J.E. 1938b. The life history of the gizzard worm (*Cheilospirura hamulosa*) and its mode of transmission to chickens, with special reference to Hawaiian conditions. Livro Jubilar Prof. Travassos 3:11-19. Rio de Janeiro, Brazil.

Alicata, J.E. 1939a. Poultry parasites. Hawaii Agric. Exp. Stn. Rep. 1938, 79-82.

Alicata, J.E. 1939b. Preliminary note on the life history of *Subulura brumpti*, a common cecal nematode of poultry in Hawaii. J. Parasitol. 25: 179-180.

Alicata, J.E. 1940. The life cycle of *Postharmostomum gallinum*, the cecal fluke of poultry. J. Parasitol. 26:135-143.

Alicata, J.E. 1947. Parasites and parasitic diseases of domestic animals in the Hawaiian Islands. Pac. Sci. 1:69-84.

Alicata, J.E. 1962. Life cycle and developmental stages of *Philophthalmus gralli* in the intermediate and final hosts. J. Parasitol. 48:47-54.

Alicata, J.E. 1964. Parasitic infections of man and animals in Hawaii. Hawaii Agric. Exp. Stn. Tech. Bull. 61.

Alicata, J.E. 1969. Parasites of man and animals in Hawaii. Basel, Switzerland: S. Karger.

Alicata, J.E., and E. Chang. 1939. The life history of *Hymenolepis exigua*, a cestode of poultry in Hawaii. J. Parasitol. 25:121-127.

Alicata, J.E., and H.L. Ching. 1960. On the infection of birds and mammals with the cercaria and metacercaria of the eye-fluke, *Philophthalmus*. J. Parasitol. 46:16.

Alicata, J.E., L. Kartman, and H.I. Fisher. 1948. Wild birds as possible carriers of poultry parasites. Hawaii Agric. Exp. Stn. Rep. 1946-1948, 104-105.

Alicata, J.E., F.G. Holdaway, J.H. Quisenberry, and D.D. Jensen. 1946. Observations on the comparative efficacy of certain old and new insecticides in the control of lice and mites of chickens. Poultry Sci. 15:376-380.

Amadon, D. 1950. The Hawaiian honeycreepers (Aves, Drepaniidae). Am. Mus. Nat. Hist. Bull. 95: 151-262.

American Ornithologists' Union. 1983. Check-list of North American birds. Lawrence, Kansas: Allen Pr., Inc.

Amerson, A.B., Jr. 1966. Ornithodoros capensis (Acarina: Argasidae) infesting sooty tern (Sterna fuscata) nasal cavities. J. Parasitol. 52: 1220-1221.

Arnall, L., and I.F. Keymer. 1975. Bird diseases. Neptune City, New Jersey: T.F.H. Pub., Inc.

Ash, J.S. 1960. A study of the Mallophaga of birds with particular reference to their ecology. Ibis 102:93-110.

Avery, R.A. 1966. Helminth parasites of wildfowl from Slimbridge, Gloucestershire. I. Parasites of captive Anatidae. J. Helminthol. 40:269-280.

Baker, E.W., and G.H. Wharton. 1952. An introduction to acarology. New York: MacMillan Co.

Baker, J.R., G.F. Bennett, G.W. Clark, and M. Laird. 1972. Avian blood coccidians. Adv. Parasitol. 10:1-30.

Baldwin, P.H. 1941. Report to the Superintendent of Hawaii Volcanoes National Park, 2 August. Typescript.

Baldwin, P.H. 1948. Discovery of tapeworm parasites in three genera of Hawaiian honey suckers. Elepaio 9:29.

Banko, P.C. 1974. Report on alala (Corvus tropicus). Natl. Park Serv., Hawaii Volcanoes Natl. Park. Typescript.

Banko, P.C., and D.A. Manuwal. 1982. Life history, ecology, and management of nene (Branta sandvicensis) in Hawaii Volcanoes and Haleakala National Parks. Final Rep., Natl. Park Serv.

Contract CX-8000-8-0005. Seattle: Univ. Wash. Coop. Natl. Park Resour. Stud. Unit.

Banko, W.E. 1980. History of endemic Hawaiian birds. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. 026/10. Honolulu: Univ. Hawaii.

Bennett, G.F., E.C. Greiner, and W. Threlfall. 1976. Protozoans. In Wildlife Diseases, ed. L.A. Page, 25-33. New York: Plenum Pub. Co.

Bequaert, J.C. 1941. The Hippoboscidae of Oceania (Diptera). B.P. Bishop Mus. Occ. Pap. 16:247-292.

Berger, A.J. 1981. Hawaiian birdlife. 2nd ed. Honolulu: Univ. Pr. Hawaii.

Bice, C.M. 1932. Poultry diseases common in Hawaii. Hawaii Agric. Exp. Stn. Circ. 5.

Bohart, R.M., and R.K. Washino. 1978. Mosquitoes of California. Univ. Calif. Agric. Sci. Pub. Berkeley.

Box, E.D. 1970. Atoxoplasma associated with an isosporan oocyst in canaries. J. Protozool. 17: 391-396.

Box, E.D. 1971. Lankesterella (Atoxoplasma). In Infectious and parasitic diseases of wild birds, ed. J.W. Davis, R.C. Anderson, L. Karstad, and D.O. Trainer, 309-312. Ames, Iowa: Iowa State Univ. Pr.

Box, E.D. 1977. Life cycles of two Isospora species in the canary, Serinus canarius Linnaeus. J. Protozool. 24:57-67.

Boyd, R.J., and R.P. Hanson. 1958. Survival of Newcastle disease virus in nature. Avian Dis. 2:82-93.

Brennan, J.M. 1965. A small collection of chiggers (Acarina: Trombiculidae) from the North Central Pacific. J. Parasitol. 51:888-892.

Brennan, J.M., and J. R. Amerson, Jr. 1971. Six new species and additional records of chiggers from the central Pacific (Acarina: Trombiculidae). J. Parasitol. 57:1311-1317.

Brock, V.E., and P.L. Breese. 1953. Duck botulism at Kaelepulu Pond, Kailua, Oahu. Elepaio 13:80-81.

Bryan, E.H., Jr. 1934. A review of the Hawaiian Diptera, with descriptions of new species. Proc. Hawaii. Entomol. Soc. 8:399-468.

Buescher, E.L. 1956. Arthropod-borne encephalitis in Japan and South-east Asia. Am. J. Public Health 46:597-600.

Butler, G.D., Jr. 1961. Insects and other arthropods from Laysan Island. Proc. Hawaii. Entomol. Soc. 17:379-387.

Butler, G.D., Jr., and R.L. Usinger. 1963. Insects and other invertebrates from Laysan Island. Atoll Res. Bull. 98.

Cavill, J.P. 1982. Viral diseases. In Diseases of cage and aviary birds, ed. M.L. Petrak, 515-527. Philadelphia, Penn.: Lea and Febiger.

Ching, H.L. 1961. The development and morphological variation of Philophthalmus gralli Mathis and Leger, 1910, with a comparison of species of Philophthalmus Looss, 1899. Proc. Helminthol. Soc. Wash. 28:130-138.

Chu, G.W.T.C., and C.E. Cutress. 1954. Austrobilharzia variglandis (Miller and Northup, 1926) Penner, 1953, (Trematoda: Schistosomatidae) in Hawaii with notes of its biology. J. Parasitol. 40:515-523.

Cid del Prado Vera, I., A.R. Maggenti, and C. van Riper III. In press. New species of Spiruridae (Nemata: Spirurida) from endemic Hawaiian honeycreepers (Passeriformes: Drepanididae), the Japanese white-eye (Passeriformes: Zoosteropidae [sic]) and a new species of Acuariidae (Nemata: Spirurida) from the Japanaes white-eye collected on the island of Hawaii. Proc. Helminthol. Soc. Wash.

Coleman, P.H. 1978. Arbovirus infections. In Diseases of poultry, ed. M.S. Hofstad, B.W. Calnek, C.F. Helmboldt, W.M. Reid, and H.W. Yoder, Jr., 654-659. Ames, Iowa: Iowa State Univ. Pr.

Cook, R.S. 1971a. Haemoproteus Kruse 1890. In Infectious and parasitic diseases of wild birds, ed. J.W. Davis, R.C. Anderson, L. Karstad, and D.O. Trainer, 300-308. Ames, Iowa: Iowa State Univ. Pr.

Cook, R.S. 1971b. Leucocytozoon Danilewsky 1980. In Infectious and parasitic diseases of wild birds, ed. J.W. Davis, R.C. Anderson, L. Karstad, and D.O. Trainer, 291-299. Ames, Iowa: Iowa State Univ. Pr.

Cram, E.B. 1927. Bird parasites of the nematode suborders Strongylata, Ascaridata, and Spirurata. U.S. Nat. Mus. Bull. 140.

Cram, E.B. 1931. Developmental stages of some nematodes of the Spiruroidea parasitic in poultry and game birds. U.S. Dep. Agric. Tech. Bull. 227.

Crosskey, R.W. In press. Geographical distribution. In Blackflies: the future for biological methods in integrated control, ed. M. Laird. London: Academic Pr.

Cuckler, A.C., and J.E. Alicata. 1944. The life history of Subulura brumpti, a cecal nematode of poultry in Hawaii. Trans. Am. Microscop. Soc. 63: 345-347.

Eddinger, C.R. 1967. A study of the breeding behavior of the mynah (Acridotheres tristis L.). Elepaio 28:1-5, 11-15.

Evans, G.O., J.G. Sheals, and D. MacFarlane. 1961. The terrestrial acari of the British Isles. London: Trustees Brit. Mus.

Fain, A., and A.B. Amerson, Jr. 1968. Two new heteromorphic deutonymphs (Hypopi) (Acarina: Hypoderidae) from the great frigatebird (Fregata minor). J. Med. Entomol. 5:320-324.

Fain, A., and M.L. Goff. 1980. Speleognathine mites (Acari: Ereynetidae) from birds in the Hawaiian Islands, with descriptions of a new species. J. Med. Entomol. 17:506-508.

Fisher, H.I., and P.H. Baldwin. 1947. Notes on the red-billed leiothrix in Hawaii. Pac. Sci. 1: 45-51.

Garnham, P.C.C. 1966. Malaria parasites and other Haemosporidia. Oxford: Blackwell Sci. Pub.

Garrett, L.E., and F.H. Haramoto. 1967. A catalog of Hawaiian Acarina. Proc. Hawaii. Entomol. Soc. 19: 381-414.

Goble, F.C., and H.L. Kutz. 1945. The genus Dispharynx (Nematoda: Acuariidae) in galliform and passeriform birds. J. Parasitol. 31:323-331.

Goff, M.L. 1971. New records of chiggers (Acarina, Trombiculidae) from the Northwestern Hawaiian Islands. J. Med. Entomol. 8:456.

Goff, M.L. 1977. A new species of Toritrombicula (Acarina: Trombiculidae) from the Pacific golden plover in the Hawaiian Islands. J. Med. Entomol. 13:735-737.

Goff, M.L. 1980. Mites (Chelicerata: Acari) parasitic on birds in Hawaii Volcanoes National Park. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. 29. Honolulu: Univ. Hawaii.

Goff, M.L. 1984. Three new species and new records of chiggers (Acari: Trombiculidae) from the Northwestern Hawaiian Islands. J. Med. Entomol. 21:257-262.

Goff, M.L., and C. van Riper III. 1980. Distribution of mosquitoes (Diptera: Culicidae) on the East Flank of Mauna Loa Volcano, Hawaii. Pac. Insects 22:178-188.

Guberlet, J.E. 1926. Notes on the parasitic fauna of Hawaii. B.P. Bishop Mus. Spec. Pub. 11:29-30.

Guest, S.J. 1973. A reproductive biology and natural history of the Japanese white-eye (Zosterops japonica japonica) in urban Oahu. Univ. Hawaii Island Ecosys. Tech. Rep. 29.

Hammon, W. McD., G.E. Sather, and H.E. McClure. 1958. Serologic survey of Japanese B encephalitis virus infection in birds in Japan. Am. J. Hyg. 67:118-133.

Hanson, R.P. 1978. Newcastle disease. In Diseases of poultry, ed. M.S. Hofstad, B.W. Calnek, C.F. Helmboldt, W.M. Reid, and H.W. Yoder, Jr., 513-535. Ames, Iowa: Iowa State Univ. Pr.

Hardy, D.E. 1952. Additions and corrections to Bryan's check list of the Hawaiian Diptera. Proc. Hawaii. Entomol. Soc. 14:443-484.

Haugen, A.D. 1952. Trichomoniasis in Alabama mourning doves. J. Wildl. Manage. 16:149-164.

Henshaw, H.W. 1902. Birds of the Hawaiian Islands, being a complete list of the birds of the Hawaiian possessions, with notes on their habits. In Hawaiian almanac and annual for 1902, 54-106. Honolulu: Thos. G. Thrum.

Herman, C.M., and E.E. Wehr. 1954. The occurrence of gizzard worms in Canada geese. J. Wildl. Manage. 18:509-513.

Herman, C.M., H.A. Jankiewicz, and R.W. Saarni. 1942. Coccidiosis in California quail. Condor 44:168-171.

Hofstad, M.S., B.W. Calnek, C.F. Helmboldt, W.M. Reid, and H.W. Yoder, Jr. 1978. Diseases of poultry. Ames, Iowa: Iowa State Univ. Pr.

Howitt, B.F., H.R. Dodge, L.K. Bishop, and R.H. Gorrie. 1948. Virus of eastern equine encephalomyelitis isolated from chicken mites (Dermanyssus gallinae) and chicken lice (Eomenacanthus stramineus). Proc. Soc. Exp. Biol. Med. 68:622-625.

Hwang, J.C., N. Tolgay, W.T. Shalkop, and D.S. Jaquette. 1961. Case report--Dispharynx nasuta causing severe proventriculitis in pigeons. Avian Dis. 5:60-65.

Illingsworth, J.F. 1916. Notes on the hen flea ("Echidnophaga gallinacea" Westw.). Proc. Hawaii. Entomol. Soc. 3:252-254.

Illingsworth, J.F. 1928. Lice affecting poultry in Hawaii. Proc. Hawaii. Entomol. Soc. 7:41-42.

Illingsworth, J.F. 1931. Manson's eyeworm distributed by English sparrow. Proc. Hawaii. Entomol. Soc. 7:461.

Karstad, L. 1971. Arboviruses. In Infectious and parasitic diseases of wild birds, ed. J.W. Davis, R.C. Anderson, L. Karstad, and D.O. Trainer, 17-21. Ames, Iowa: Iowa State Univ. Pr.

Kartman, L. 1949. Observations on the Haemoproteus of pigeons in Honolulu, Hawaii. Pac. Sci. 3:127-132.

Kartman, L. 1951. Notes on Tetrameres sp. (Nematoda, Spiruroidea) parasitic in the English sparrow in Hawaii. Pac. Sci. 5:252-255.

Kear, J., and A.J. Berger. 1980. The Hawaiian goose: an experiment in conservation. Vermillion, S. Dakota: Buteo Books.

Kemp, R.L., and W.T. Springer. 1978. Histomoniasis. In Diseases of poultry, ed. M.S. Hofstad, B.W. Calnek, C.F. Helmboldt, W.M. Reid, and H.W. Yoder, Jr., 832-840. Ames, Iowa: Iowa State Univ. Pr.

Keymer, I.F. 1982a. Mycoses. In _Diseases of cage and aviary birds_, ed. M.L. Petrak, 599-605. Philadelphia, Penn.: Lea and Febiger.

Keymer, I.F. 1982b. Parasitic diseases. In _Diseases of cage and aviary birds_, ed. M.L. Petrak, 535-598. Philadelphia, Penn.: Lea and Febiger.

Kingston, N. 1978. Trematodes. In _Diseases of poultry_, ed. S. Hofstad, B.W. Calnek, C.F. Helmboldt, W.M. Reid, and H.W. Yoder, Jr., 759-782. Ames, Iowa: Iowa State Univ. Pr.

Kissling, R.E., R.W. Chamberlain, R.K. Sikes, and M.E. Eidson. 1954. Studies on the North American arthropod-borne encephalitides. III. Eastern equine encephalitis in wild birds. _Am. J. Hyg._ 60:251-265.

Kocan, R.M., and W. Banko. 1974. Trichomoniasis in the Hawaiian barred dove. _J. Wildl. Dis._ 10:359-360.

Kocan, R.M., and C.M. Herman. 1971. Trichomoniasis. In _Infectious and parasitic diseases of wild birds_, ed. J.W. Davis, R.C. Anderson, L. Karstad, and D.O. Trainer, 282-290. Ames, Iowa: Iowa State Univ. Pr.

Kohls, G.M., D.E. Sonenshine, and C.M. Clifford. 1965. The systematics of the subfamily Ornithodorinae (Acarina: Argasidae). II. Identification of the larvae of the Western Hemisphere and descriptions of three new species. _Annals Entomol. Soc. Am._ 58:331-364.

Krantz, G.W. 1978. _A manual of acarology_. Corvallis, Ore.: Oregon State Univ. Book Stores, Inc.

Kudo, R.S. 1966. _Protozoology_. Springfield, Ill.: C.C. Thomas, Pub.

Lainson, R. 1959. _Atoxoplasma_ Garnham, 1950, as a synonym for _Lankesterella_ Labbe, 1899. Its life cycle in the English sparrow (_Passer domesticus domesticus_, Linn.). _J. Protozool._ 6:360-371.

Lainson, R. 1960. The transmission of _Lankesterella_ (= _Atoxoplasma_) in birds by the mite _Dermanyssus gallinae_. _J. Protozool._ 7:321-322.

Laird, M., and C. van Riper, III. 1981. Questionable reports of _Plasmodium_ from birds in Hawaii, with the recognition of _P. relictum_ ssp. _capistranoae_ (Russell, 1932) as the avian malaria parasite there. In Parasitological Topics, ed. E.V. Canning, 159-165. Soc. of Cap. Protozool. Spec. Pub. 1. Lawrence, Kans.: Allen Pr.

Levine, N.D. 1980. Nematode parasites of domestic animals and of man. Minneapolis, Minn.: Burgess Pub. Co.

Levine, N.D. 1982a. Isospora vanriperorum n.nom. for I. cardinalis Levine, Van Riper & Van Riper, 1980, Preoccupied. J. Protozool. 29:653.

Levine, N.D. 1982b. The genus Atoxoplasma (Protozoa, Apicomplexa). J. Parasitol. 68:719-723.

Levine, N.D., and S. Kantor. 1959. Check list of blood parasites of birds of the order Columbiformes. Wildl. Dis. 1:1-38.

Levine, N.D., S. van Riper, and C. van Riper, III. 1980. Five new species of Isospora from Hawaiian birds. J. Protozool. 27:258-259.

Lewin, V., and J.C. Holmes. 1971. Helminths from the exotic game birds of the Puuwaawaa Ranch, Hawaii. Pac. Sci. 25:372-381.

Lewin, V., and J.L. Mahrt. 1983. Parasites of Kalij pheasants (Lophura leucomelana) on the island of Hawaii. Pac. Sci. 37:81-83.

Locke, L.N., W.O. Wirtz, II, and E.E. Brown. 1965. Pox infection and a secondary cutaneous mycosis in a red-tailed tropicbird (Phaethon rubricauda). Wildl. Dis. Assn. Bull. 1:60-61.

Loomis, E.C. 1978. External parasites. In Diseases of poultry, ed. M.S. Hofstad, B.W. Calnek, C.F. Helmboldt, W.M. Reid, and H.W. Yoder, Jr., 667-704. Ames, Iowa: Iowa State Univ. Pr.

Maa, T.C. 1966. Studies in Hippoboscidae (Diptera). Part 1. Pac. Insects Monogr. 10:1-148.

Maa, T.C. 1967. Diptera: Hippoboscidae. Insects Micronesia 14:267-271.

Maa, T.C. 1968. Records of Hippoboscidae (Diptera) from the central Pacific. J. Med. Entomol. 5:325-328.

Maa, T.C. 1969a. A revised checklist and concise host index of Hippoboscidae (Diptera). Pac. Insects Monogr. 20:261-299.

Maa, T.C. 1969b. Synopses of the genera Ornithophila and Ornithoctona with remarks on their habitat diversification. Pac. Insects Monogr. 20:1-23.

McDonald, M.E. 1981. Key to trematodes reported in waterfowl. U.S. Fish Wildl. Serv. Resour. Pub. 142.

MacFie, J.W.S., and J.G. Thompson. 1929. A trypanosome of the canary (Serinus canarius Koch). Trans. Royal Soc. Trop. Med. Hyg. 23:5-6, 185-191.

Martin, W.E. 1958. The life histories of some Hawaiian heterophyid trematodes. J. Parasitol. 44:305-323.

Munro, G.C. 1969. Birds of Hawaii. Rutland, Vt.: C.E. Tuttle Co., Inc.

Navvab Gojrati, H.A. 1970. Epizootiological survey of avian malaria in the Hawaiian Islands. Ph.D. Diss. Honolulu: Univ. Hawaii.

Noble, E.R., and G.A. Noble. 1971. Parasitology. Philadelphia, Penn.: Lea and Febiger.

Okamoto [sic = Okimoto], B. 1975. Parasites of the Pacific golden plover and their use as biological markers. Elepaio 36:53-54.

O'meara, D.C., and J.F. Witter. 1971a. Aspergillosis. In Infectious and parasitic diseases of wild birds, ed. J.W. Davis, R.C. Anderson, L. Karstad, and D.O. Trainer, 153-162. Ames, Iowa: Iowa State Univ. Pr.

O'meara, D.C., and J.F. Witter. 1971b. Candidiasis. In Infectious and parasitic diseases of wild birds, ed. J.W. Davis, R.C. Anderson, L. Karstad, and D.O. Trainer, 163-169. Ames, Iowa: Iowa State Univ. Pr.

Palmer, S.F., and D.O. Trainer. 1971. Newcastle disease. In Infectious and parasitic diseases of wild birds, ed. J.W. Davis, R.C. Anderson, L. Karstad, and D.O. Trainer, 3-16. Ames, Iowa: Iowa State Univ. Pr.

Pemberton, C.E. 1943. Insects and other arthropods of medical interest in Hawaii. Hawaii Med. J. 2:191-194.

Perkins, R.C.L. 1893. Notes on collecting in Kona, Hawaii. Ibis 1893:101-114.

Perkins, R.C.L. 1903. Vertebrata. In Fauna Hawaiiensis, ed. D. Sharp, Vol. 1, Part IV, 365-466. Cambridge, England: The Univ. Pr.

Quisenberry, W.B., and G.D. Wallace. 1959. Arthropod-borne virus encephalitis potentials in Hawaii. Hawaii Med. J. 19:29-31.

Radovsky, F.J. 1971. Notes and exhibitions: Bakericheyla chanayi. Proc. Hawaii. Entomol. Soc. 21:10.

Raper, K.B., D.I, Fennell, and P.K.C. Austwick. 1973. The genus Aspergillus. Huntington, New York: R.E. Krieger Pub. Co.

Reid, W.M. 1978a. Cestodes. In Diseases of poultry, ed. M.S. Hofstad, B.W. Calnek, C.F. Helmboldt, W.M. Reid, and H.W. Yoder, Jr., 737-758. Ames, Iowa: Iowa State Univ. Pr.

Reid, W.M. 1978b. Coccidiosis. In Diseases of poultry, ed. M.S. Hofstad, B.W. Calnek, C.F. Helmboldt, W.M. Reid, and H.W. Yoder, Jr., 784-815. Ames, Iowa: Iowa State Univ. Pr.

Rosen, M.N. 1971. Botulism. In Infectious and parasitic diseases of wild birds, ed. J.W. Davis, R.C. Anderson, L. Karstad, and D.O. Trainer, 100-117. Ames, Iowa: Iowa State Univ. Pr.

Rothschild, M., and T. Clay. 1957. Fleas, flukes, and cuckoos. New York: MacMillan and Co.

Ruff, M.D. 1978. Nematodes and acanthocephalans. In Diseases of poultry, ed. M.S. Hofstad, B.W. Calnek, C.F. Helmboldt, W.M. Reid, and H.W. Yoder, Jr., 705-736. Ames, Iowa: Iowa State Univ. Pr.

Schmidt, G.D. 1969. Acanthocephala as agents of disease in wild mammals. Wildl. Dis. 53:1-10.

Schmidt, G.D., and R.E. Kuntz. 1977. Revision of Mediorhynchus Van Cleave 1916 (Acanthocephala) with a key to species. J. Parasitol. 63:500-507.

Schwabe, C.W. 1950. Studies on Oxyspirura mansoni, the tropical eyeworm of poultry. III. Preliminary observations on eyeworm pathogenicity. Am. J. Vet. Res. 11:286-290.

Schwabe, C.W. 1951. Studies on Oxyspirura mansoni, the tropical eyeworm of poultry. II. Life history. Pac. Sci. 5:18-35.

Schwartz, C.W., and E.R. Schwartz. 1949. The game birds in Hawaii. Honolulu: Hawaii Board Comm. Agric. For., Terr. Hawaii.

Schwartz, C.W., and E.R. Schwartz. 1951. An ecological reconnaissance of the pheasants in Hawaii. Auk 68:281-314.

Schwartz, C.W., and E.R. Schwartz. 1953. Notes on the Hawaiian duck. Wilson Bull. 65:18-25.

Simons, T.R. 1983. Biology and conservation of the endangered Hawaiian dark-rumped petrel (Pterodroma phaeopygia sandwichensis). Univ. Wash. Coop. Natl. Park Resour. Stud. Unit Tech. Rep. 83-2. Seattle: Univ. Wash.

Smith, H.E. 1973a. A rhinonyssid mite in atypical loci of estrildine finches in Hawaii. J. Parasitol. 59:1148.

Smith, H.E. 1973b. Syngamus trachea: a first report in Hawaii. Elepaio 33:95-96.

Smith, H.E., and S.J. Guest. 1974. A survey of internal parasites of birds on the western slopes of Diamond Head, Oahu, Hawaii 1972-1973. Univ. Hawaii Island Ecosys. Tech. Rep. 37. Honolulu: Univ. Hawaii.

Sulkin, S.E., and E.N. Izumi. 1947. Isolation of western equine encephalomyelitis virus from tropical fowl mites, Liponyssus bursa (Berlese). Proc. Soc. Exp. Biol. Med. 66:249-250.

Swanson, L.E. 1939. A note on the parasitic fauna of the Hawaiian Islands. Proc. Helminthol. Soc. Wash. 6:29-30.

Takahashi, M., C.E. Yunker, C.M. Clifford, W. Nakano, N. Fujino, K. Tanifuji, and L.A. Thomas. 1982. Isolation and characterization on Midway Virus: a new tick-borne virus related to Nyamanini. J. Med. Virol. 10:181-193.

Tempelis, C.H., R.O. Hayes, A.D. Hess, and W.C. Reeves. 1970. Blood-feeding habits of four species of mosquito found in Hawaii. Am. J. Trop. Med. Hyg. 19:335-341.

Thompson, G.B. 1948. Mallophaga collected by the Tanager Expedition. B.P. Bishop Mus. Occ. Pap. 19: 195-200.

Throp, J.L. 1970. The Laysan finch bill in the Honolulu Zoo. Elepaio 31:31-34.

Todd, K.S., Jr., and D.M. Hammond. 1971. Coccidia of Anseriformes, Galliformes, and Passeriformes. In Infectious and parasitic diseases of wild birds, ed. J.W. Davis, R.C. Anderson, L. Karstad, and D.O. Trainer, 234-281. Ames, Iowa: Iowa State Univ. Pr.

Tomich, P.Q. 1967. Arthropoda associated with a nest of the Hawaiian crow. Proc. Hawaii. Entomol. Soc. 19:431-432.

Turner, E.C., Jr. 1971. Fleas and lice. In Infectious and parasitic diseases of wild birds, ed. J.W. Davis, R.C. Anderson, L. Karstad, and D.O. Trainer, 175-184. Ames, Iowa: Iowa State Univ. Pr.

T-W-Fiennes, R.N. 1982. Diseases of bacterial origin. In Diseases of cage and aviary birds, ed. M.L. Petrak, 497-515. Philadelphia, Penn.: Lea and Febiger.

U.S. Department of Agriculture and Southeastern Cooperative Wildlife Disease Study. 1980. APHIS/SCWDS Velogenic viscerotropic Newcastle disease surveillance Miami, Florida; Hawaii, Maui, and Kauai, Hawaii; San Diego, California; and Portland, Oregon (9/10/80-10/9/80). Spons. by Veterin. Serv. Anim. Plant Health Inspect. Serv., U.S. Dept. Agric., Washington, D.C. in collab. Southeast. Coop. Wildl. Disease Stud. Coll. Vet. Med., Univ. Georgia, Athens.

van Riper, C., III. 1975. Parasites of the Hawaii amakihi (Loxops virens virens). Univ. Hawaii Island Ecosys. Tech. Rep. 62. Honolulu: Univ. Hawaii.

van Riper, C., III. 1978. The breeding ecology of the amakihi (Loxops virens) and palila (Psittirostra bailleui) on Mauna Kea, Hawaii. Ph.D. Diss. Honolulu: Univ. Hawaii.

van Riper, C., III. 1980. Observations on the breeding of the palila (Psittirostra bailleui) of Hawaii. Ibis 122:462-475.

van Riper, C., III, and R.D. Barbee. 1978. Dark-rumped petrel at Hawaii Volcanoes National Park. Bird-Banding 49:372.

van Riper, C., III, S.G. van Riper, M.L. Goff, and M. Laird. In press. The epizootiology and ecological significance of malaria in Hawaiian landbirds. Ecology.

Vogue, M., and B.S. Davis. 1953. Studies on the cestode genus Anonchotaenia (Dilepididae, Paruterininae) and related forms. Univ. Calif. Pub. Zool. 59.

Wallace, G.D., D. Auai, A. Oda, R.E. Kissling, and W.B. Quisenberry. 1964. Arthropod-borne virus survey on the island of Oahu, Hawaii. Hawaii Med. J. 23: 364-386.

Wardle, R.A., J.A. McLeod, and S. Radinovsky. 1974. Advances in the zoology of tapeworms, 1950-1970. Minneapolis, Minn.: Univ. Minn. Pr.

Warner, R.E. 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. Condor 70:101-120.

Washino, R.K., and C.H. Tempelis. 1983. Mosquito host bloodmeal identification: methodology and data analysis. Ann. Rev. Entomol. 28:179-201.

Wehr, E.E. 1971. Nematodes. In Infectious and parasitic diseases of wild birds, ed. J.W. Davis, R.C. Anderson, L. Karstad, and D.O. Trainer, 185-233. Ames, Iowa: Iowa State Univ. Pr.

Williams, I.C. 1960. The anatomy and some aspects of the biology of Urotocus rossittensis (Muhling, 1898) Looss, 1899 (Trematoda: Brachylaemidae) from the bursa Fabricii of the rock-pipit, Anthus spinoletta petrosus (Montagu). Ann. Mag. Nat. Hist. 13:65-86.

Wilson, N. 1964a. Ixodes laysanensis, a new species of tick from birds on Laysan Island (Metastigmata: Ixodidae). J. Med. Entomol. 1:165-168.

Wilson, N. 1964b. New records and descriptions of Rhinonyssidae, mostly from New Guinea (Acarina: Mesostigmata). Pac. Insects 6:357-388.

Wilson, N. 1966. New records and a new species of Mesonyssus (Mesostigmata: Rhinonyssidae) from pigeons and doves (Columbiformes: Columbidae). J. Parasitol. 52:1210-1213.

Yeager, R.H., and C.A. Gleiser. 1946. Trichomonas and Hemoproteus infections and the experimental use of DDT in the control of ectoparasites in a flock of

Signal Corps pigeons in the Territory of Hawaii. J. Am. Vet. Med. Assn. 109:204-207.

Zimmerman, E.C. 1944. A case of bovine auricular myiasis and some ectoparasites new to Hawaii. Proc. Hawaii. Entomol. Soc. 12:119-200.

Zimmerman, E.C. 1948. Insects of Hawaii. Vol. 1, Introduction. Honolulu: Univ. Hawaii Pr.

Zimmerman, E.C. 1948. Insects of Hawaii. Vol. 2, Apterigota to Thysanoptera. Honolulu: Univ. Hawaii Pr.

11.

STATUS, RESEARCH AND MANAGEMENT NEEDS FOR ALIEN BIOTA: A SUMMARY AND COMMENTARY

Ronald L. Walker

The speakers in this session discussed the adverse effects of alien organisms on native Hawaiian biota. Introduced invertebrates are known to be ubiquitous and abundant. Spec'es establishment appears to progress geometrically as new introductions create new niches, and the effects on native forms are often vital, e.g. the disruption of pollination systems. While aliens need to be controlled, caution is advised as undesirable impacts can occur through use of chemical and biological methods. Solutions to problems involving invertebrates were suggested, including:

1. Don't despair of solving the problems; they need to be addressed.
2. "Further research is necessary."
3. Biological control should be used, but judiciously.
4. Quarantine procedures need improvement.
5. Public education is vital to program understanding and acceptance.

The first introduced plants were brought to the Islands by the Hawaiians over 1,500 years ago. Early explorers, settlers, and agriculturalists established many others, and foresters and horticulturalists also contributed new species. Problems associated with agriculture and horticulture are currently more important than those involving native ecosystems. Various land uses create environments for pest plants. Introduced plants may shade out native plants, constitute fuel for fires, and compete with native plants for water and energy. Solutions to problems with alien plants include preventing new introductions, restoring native plants, better public education, and more interagency cooperation.

Adverse effects attributable to alien vertebrates can be classified as:

1. Predation--animals upon animals;
2. Depredation--animals upon plants;

3. Competition between aliens and native biota. Alien vertebrates also serve as vectors of disease and weed dispersal and degrade plant and animal habitats. Actions needed include continued research; better quarantine procedures; the control of herbivores (by fencing, hunting, and/or trapping); and the controlled use of toxicants. Better coordination among administrators, researchers, and managers, and more cooperation among agencies are needed. Increased international communication and cooperation among those experienced with introduced vertebrate problems on islands might enhance efficiency and result in more rapid solutions.

The ancestors of today's native birds brought endoparasites and ectoparasites with them upon arriving in Hawai'i. New diseases and parasites have been added since. The present situation is not as bad as it could be in the future. Intermediate hosts and vectors maintain and transmit diseases and parasites and must be minimized. Other solutions include biological controls, additional research on individual islands, and the prevention of new parasite and disease establishment via a rigorous quarantine.

All speakers seemed in agreement that aliens are undesirable, that they are widespread, and that we are not doing enough to control them. The call for additional studies of native-alien interactions was loud and clear.

My views are as follows: Aliens are now a natural part and parcel of Hawaiian ecosystems and probably always will be, whether we like it or not. We know the problems and demand immediate solutions. However, the government cannot be all things to all people. We have to use the system and not fight it. We have to ask where the money is coming from and whether present governmental systems are responsive to alien problems. It is more productive to do things through channels than to make idealistic, unrealistic demands. Above all, we need to set priorities and implement actions starting from the top down. We cannot afford adversary relationships among the governmental, academic, and scientific sectors. We have to work together. It is said that the definition of a mummy is an Egyptian who is strapped for time. Everyone is busy; we cannot afford to argue. Rather, we have to make the best use of our time in seeking solutions to major problems.

III. ECOSYSTEM MONITORING, RESTORATION, AND MANAGEMENT IN HAWAI'I

12.

VEGETATION RESPONSE WITHIN EXCLOSURES IN HAWAI'I: A REVIEW

Lloyd L. Loope and Paul G. Scowcroft

ABSTRACT

Exclosure studies have been used to great advantage in the Hawaiian Islands to evaluate and demonstrate impacts of alien vertebrate herbivores upon native vegetation. Information presented for 50 exclosures, mostly on Hawai'i and Maui, shows a wide range of vegetation responses. In most situations, native biota hold their own or increase following removal of vertebrate damage, but the chance of recovery becomes reduced as the extent of degradation increases. Displacement by alien grasses appears to be the most significant factor inhibiting reproduction of native species in areas other than rain forest. The intact native vegetation in "natural exclosures" shows that damage by alien vertebrates is a prerequisite for large-scale invasion of alien plant species. Priorities for the future include continuing maintenance and evaluation of existing exclosures and establishment of new ones in leeward low and middle elevation ecosystems. Comprehensive monitoring should be carried out to document biological and physical changes resulting from vertebrate herbivore exclusion aided by large fencing projects.

INTRODUCTION

Construction of "exclosures" with fencing to exclude alien vertebrate herbivores from small areas has proved to be a highly useful tool in allowing, demonstrating, and/or determining vegetation recovery from grazing, browsing, trampling, digging, etc. by these animals. Exclosures are commonly used by land managers throughout the world, both on islands and in continental situations (Tiedemann and Berndt 1972; Jane and Pracy 1974; Marquis 1974; Lock 1977; Kightley and Smith 1978; Coblentz 1977). In Hawai'i, exclosures have most frequently been used in areas where native vegetation persists. We present in this paper an inventory of exclosures in the State of Hawai'i known to us; review objectives and accomplishments of their establishment; review methods and frequency of vegetation monitoring used; summarize vegetation response under protection; examine the special case of "natural exclosures;" and explore future needs.

INVENTORY OF HAWAIIAN EXCLOSURES

We have been able to obtain information on 51 exclosures in the State of Hawai'i, most of which are on the islands of Hawai'i (27) and Maui (18). These exclosures have been constructed by the U.S. National Park Service (NPS, 22 in number), the Hawai'i Department of Land and Natural Resources (DLNR, 20), and other institutions. Table 1 lists these exclosures and provides the following information: location (island, volcanic mass, and U.S. Geological Survey [USGS] quadrangle map); responsible agency; vegetation zone, according to the system of Ripperton and Hosaka (1942); year constructed; approximate size in hectares; purpose of establishment; brief characterization of vegetation response to date; and source of information. Table 2 gives a simplified version of the Ripperton and Hosaka (1942) classification scheme for zonal vegetation in Hawai'i.

EXCLOSURE OBJECTIVES AND THEIR ACCOMPLISHMENT

The reasons for building the exclosures listed in table 1 fall into broad and often overlapping categories. In this section, we discuss some prime examples of how the 4 objectives listed below were or were not met.

Demonstrate Impacts of Alien Vertebrate Herbivores

Exclosure HKi-1 was a major public relations success for Hawai'i Volcanoes National Park (HAVO) early in its fencing/feral goat (*Capra hircus*) eradication program. Within 2 years of its construction, an endemic species, *Canavalia kauensis* appeared, which had apparently survived 150 years of goat browsing through seeds lying dormant in the soil (St. John 1972; Baker and Reeser 1972). This discovery gave tremendous momentum to the goat control program, which was sustained even though the response of native species in other exclosures was less dramatic. Similarly, prompt and excellent recovery of vegetation damaged by feral pigs (*Sus scrofa*) in an exclosure (HKi-5) in a rain forest area near Napau Crater (Katahira 1980) gave impetus to an accelerated program of pig control at HAVO.

Study Recovery Potential of Animal-damaged Ecosystems

Included in this objective are studies of reproduction, survival, and growth of native plants; changes

Table 1. Inventory of exclosures in the Hawaiian Islands.

Name/Descriptor	Purpose	Findings	References/Sources
Sandalwood Sanctuary HMK-1-DLNR-E2-68-Ø.8-Ahumoa (NW)	Protection of concentration of sandalwood trees	Sandalwood trees have flourished and are reproducing by rootsuckers but not seedlings	DLNR-DOFAW (Hilo)
Kaluamakani HMK-2-DLNR/SCS-E2-63-Ø.4-`Umikoa (SW)	Demonstration area to show adverse effect of feral and mouflon sheep on vegetation	Mamane reproducing inside but not outside exclosure. Plant cover greater inside	Scowcroft and Giffin 1983
Pu`u Nanaha HMK-3-DLNR/SCS-E2-63-Ø.4-Ahumoa (NE)	Same as Kaluamakani	Same as Kaluamakani	Scowcroft and Giffin 1983
Pu`u Kole HMK-5-DLNR/SCS-E2-63-Ø.4-Mauna Kea (SE)	Same as Kaluamakani	Same as Kaluamakani	Scowcroft and Giffin 1983
Kahinahina HMK-5-DLNR/SCS-E2-63-Ø.4-Mauna Kea (SE)	Same as Kaluamakani	Little difference evident between protected and unprotected areas	DLNR-DOFAW files
Wailuku HMK-6-DLNR/FS-E2-Ø.9-Mauna Kea (SE)	Same as Kaluamakani; and test methods for regenerating silversword and mamane	Same as Kaluamakani; planting of silversword and mamane successful; direct sowing of mamane seeds a marginal practice	Scowcroft and Giffin 1983; Scowcroft 1981
Pu`u o Kauha HMK-7-FS-E2-72-Ø.3-Ahumoa (SE)	Determine effect of feral and mouflon sheep on mamane and other plant species	Feral sheep suppress mamane reproduction and other preferred browse species	Scowcroft and Giffin 1983

Table 1. Continued.

Name/Descriptor References/Sources	Purpose	Findings	
Hale Pohaku HMK-8-FS-E2-72-Ø.3- Mauna Kea (SW)	Same as Pu`u o Kauha	Same as Pu`u o Kauha	Scowcroft and Giffin 1983
Pu`u La`au-Mauka HMK-9-DLNR-E2-73-Ø.1- Ahumoa (NW)	Demonstrate natural recovery of mamane forest freed from sheep browsing	Rapid growth of mamane sprouts and seedlings	DLNR-DOFAW files (Hilo)
Wailuku Pen HMK-1Ø-DLNR-E2-63-Ø.1- Mauna Kea (SE)	Abandoned mouflon holding pen now a demonstration area for forest recovery	Vegetation more abundant inside pen	DLNR-DOFAW (Hilo)
Pu`u Nanaha-Mauka HMK-11-DLNR-E2-73-Ø.4- Ahumoa (NE)	Demonstrate response of vegetation to protection from sheep above tree line	Little change observed inside	DLNR-DOFAW (Hilo)
Pu`u o Kauha-Mauka HMK-12-DLNR-E2-78-2.Ø- Ahumoa (NE)	Test feasibility of reforesting by planting mamane seedlings	High survival and good growth of nursery stock	DLNR-DOFAW files (Hilo)
Pu`u Kaupakuhale HMK-13-DLNR-E2-72-Ø.4- Mauna Kea (SE)	Demonstration area above tree line to show vegetation recovery when sheep are excluded	No follow-up measurements	DLNR-DOFAW (Hilo)
Laupahoehoe HMK-14-FS-D3-75-Ø.1- Keanakolu (SW)	Study survival and growth of rooted cuttings, air-layers,and tissue culture seedlings from superior koa trees	All tissue culture seedlings died and all others lived. Some trees growing well	Skolmen 1978

Table 1. Continued.

Name/Descriptor References/Sources	Purpose	Findings	
Humu`ula HMK-15-FS-D3-77-Ø.1-Keanakolu (SW)	Test koa reforestation methods	Regeneration efforts negated by banana poka	USFS files (Skolmen, Honolulu)
Kukaiau #2 HMK-16-MKR/FS-D3-78-2.Ø-Keanakolu (NW)	Test koa reforestation methods	Excellent survival and growth of containerized koa seedlings Little natural regeneration	MKR/FS (Skolmen, Honolulu)
Koai`e Sanctuary HKo-1-DLNR-D2-5Ø-5.2-Kamuela (NW)	Protection and recovery of *Acacia koaia* and other dryland species	Seedlings of resident woody plants in the exclosure have grown well. Planted *Hibiscadelphus* barely alive	DLNR-DOFAW (Hilo)
Honua`ula HHu-1-DLNR-D3-82-Ø.4-Kailua (SE)	Study survival and growth of koa nursery stock	None to date	DLNR-DOFAW (Hilo)
Mauna Loa Strip HML-1-NPS-D3-68-Ø.1-Kilauea Crater (NE)	Determine effect of feral goats on koa reproduction. No longer maintained	Goat browsing/trampling leads to increase in production of koa suckers but suppresses their growth	Spatz and Mueller-Dombois 1973
Keauhou HML-2-BE/FS-D3-77-81.Ø-Kulani (SW)	Study stand development after soil scarification and test cultural practices	Abundant regeneration, even in unscarified areas; rapid growth; fertilization useful	Skolmen and Fujii 198Ø
Keauhou #2 HML-3-BE/DLNR-D3-8Ø-2.Ø-Kulani (SW)	Demonstrate ability of koa to recolonize a logged and grazed site	None to date	Bishop Estate (Honaunau)

Name/Descriptor References/Sources	Purpose	Findings	
Powerline HML-4-DLNR-bog-84-0.1	Protect declining population of Ka`u silversword, *Argyroxiphium kauense*	None to date	DLNR/DOFAW (Hilo)
Kukalau`ula HKi-1-NPS-A/B-68-0.1- Ka`u Desert (SW)	Determine recovery of lowland vegetation protected from goats	Appearance of new endemic species, *Canavalia kauensis*; annual alien grass replaced by alien perennials	Mueller-Dombois and Spatz 1975; Mueller-Dombois 1979, 1981
Fern Jungle HKi-2-NPS-D2-68-0.1- Volcano (NW)	Determine recovery of rain forest understory from pig damage	Modest increase of cover by native species and decrease of aliens after 13 years	Higashino and Stone 1982
Pu`u Kaone #1 HKi-3-NPS-A/B-71-0.1- Ka`u Desert (SE)	Determine recovery of lowland vegetation	Change in dominant alien grass species; large increase in the alien grass *Melinus*. Increase in total cover	Mueller-Dombois and Spatz 1975; Mueller-Dombois 1981
Pu`u Kaone #2 HKi-4-NPS-A/B-71-1.0- Ka`u Desert (SE)	Determine recovery of lowland vegetation. Used as nene pen starting in 1976	Same as above. Also large increase in the alien tree *Leucaena*	Mueller-Dombois and Spatz 1975; Mueller-Dombois 1979
Napau Crater HKi-5-NPS-D2-75-0.4- Makaopuhi Crater (NE)	Determine recovery of rain forest understory from feral pig damage	Dramatic recovery of native vegetation	Katahira (1980)
Thurston Lava Tube HKi-6-NPS-D2-81200 Volcano (NW)	Test feasibility of removal and exclusion of pigs	Pigs successfully excluded from area	NPS files (Hawaii Volcanoes N.P., Resources Mgmt.)

Table 1. Continued.

Name/Descriptor References/Sources	Purpose	Findings	
Honokahua EMa-1-NPS-E2-65-Ø.1-Nahiku (SW)	Determine recovery of mamane stand under protection from goats	Disappearance of browse line on individual trees; no reproduction	Jacobi 198Ø
Auwahi EMa-2-TNC-C2-69-5-Luala`ilua Hills (SW)	Protection of concentration of rare dryland forest tree species; determine recovery under protection from cattle	Invasion by kikuyugrass prevented reproduction of trees; deterioration of stand continued	Medeiros, Loope, and Holt, in prep.
Kalapawili grassland EMa-3-NPS-E1-74-Ø.Ø4-Nahiku (SE)	Determine result of competition between native and introduced grasses under protection after pig disturbance	Stable situation over 5-year period; native grass *Deschampsia* holding its own	Jacobi 1981
Healani EMa-4-DLNR-D3-76-Ø.2-Kaupo (NE)	Determine recovery of koa stand under protection from goat browsing	Good immediate reproduction of koa; simultaneous increase in alien grass *Melinus*	Scowcroft and Hobdy, in prep.
East Kaupo EMa-5-NPS-D3/ C2-77-3.Ø-Kaupo (NE)	Protect mixed forest from goats	Improved reproduction of *Myrsine*, *Coprosma stephanocarpa*; kikuyugrass has prevented reproduction of rare trees in lower portion	Loope, Medeiros, and Crivellone, in prep.
West Kaupo EMa-6-NPS-C2/ E2-78-Ø.1-Kaupo (NW)	Determine recovery potential of goat-damaged area	Initial dominance by alien grasses; gradual increase of native shrubs	Loope, Medeiros, and Crivellone, in prep.

Table 1. Continued.

Name/Descriptor References/Sources	Purpose	Findings	
Flattop Bog EMa-7-NPS-bog-79-Ø.2- Nahiku (SE)	Protect pig-damaged bog and allow recovery	Alien dominants have occupied bare ground and may have displaced some native bog vegetation since fencing	Loope, Medeiros, and Gagne, in prep.
Kipahulu (475Ø ft) EMa-8-NPS-D3-79-Ø.1- Nahiku (SW)	Determine recovery of `ohi`a rain forest vegetation under protection from pigs	Recovery slow	Loope, Medeiros, and Crivellone, in prep.
Kipahulu (32ØØ ft) EMa-9-NPS-D2-79-Ø.1- Kaupo (NE)	Determine recovery of koa rain forest vegetation under protection from pigs	Not remeasured yet	Loope, Medeiros, and Crivellone, in prep.
Kipahulu (22ØØ ft) EMa-1Ø-NPS-D2-79-Ø.1- Kipahulu (NW)	Determine recovery of low elevation rain forest vegetation under protection from pigs	Not remeasured yet	Loope, Medeiros and Crivellone, in prep.
Pu`u Mamane EMa-11-NPS-E2-81-Ø.4- Nahiku (SW)	Determine recovery potential of mamane stand under protection from goats	Good initial vegetative recovery; poor seedling growth and survival	Loope, Medeiros, and Crivellone, in prep.
Greensword Bog EMa-12-NPS-bog-81-Ø.2- Nahiku (SE)	Protect pig-damaged bog and allow recovery	Cover of native bog spp. increased from 4% to 39% in 2 years; no invasion of aliens as yet	Loope, Medeiros, and Gagne, in prep.

Name/Descriptor References/Sources	Purpose	Findings	
\`Iliahi EMa-13-NPS-E2-81-Ø.2-Kilohana (SE)	Determine recovery of stand of <u>Santalum haleakalai</u> under protection from goat browsing	Slow growth of vegetative root suckers; no new seedling establishment yet	Loope, Medeiros, and Crivellone, in prep.
Kaupo Dryland Ridge EMa-14-NPS-D3/ C2-81-Ø.1-Kaupo (NE)	Allow rare dryland forest to reproduce	Initial reproduction of more common tree species. Increase in alien grass cover	Loope, Medeiros, and Crivellone, in prep.
Polipoli/red Geranium EMa-15-DLNR-E2-83-Ø.5-Luala\`ilua Hills (NW)	Allow very rare <u>Geranium arboreum</u> to reproduce	Not re-evaluated yet	DLNR-DOFAW (Wailuku)
New Bog EMa-16-NPS-bog-83-Ø.2-Nahiku (SE)	Allow pig-damaged bog to recover before alien plants invade	Not remeasured yet	Loope, Medeiros, and Gagne, in prep.
Ko\`olau/orchid EMa-17-TNC/NPS-E1-84-8.1-Nahiku (SW)	Protect small population of <u>Plantanthera holochila</u>, a very rare endemic orchid	Not re-evaluated yet	Loope, Medeiros, and Crivellone, in prep.
Manawainui/Remya WMa-1-DLNR-C-82-23-Ma\`alaea (NW)	Protect very rare <u>Remya mauiensis</u> and other species of dryland forest/shrubland	No formal re-evaluation as yet	DLNR-DOFAW (Wailuku)
Kaho\`olawe #3 Kah-1-DLNR/FS/USN-A-71-Ø.2-Kaho\`olawe East (SW)	Study recovery of vegetation after goats excluded; test suitability of alien trees for erosion control	Only alien species present after fencing, mainly grasses	USFS files (Whitesell, Honolulu)

Table 1. Continued.

Name/Descriptor References/Sources	Purpose	Findings	
Kaho`olawe #4 Kah-2-DLNR/FS/USN-A-71-0.2-Kaho`olawe East	Same as Kaho`olawe #3	A few indigenous *Waltheria americana* inside only	USFS files (Whitesell, Honolulu)
Kaho`olawe #5 Kah-3-DLNR/FS/USN-A-71-0.2-Kaho`olawe West (NE)	Same as Kaho`olawe #3	Indigenous *Waltheria americana* and *Sida fallax* well represented inside and outside	USFS files (Whitesell, Honolulu)
Puhi`elelu Ridge L-1-private-C-82-.001-Lana`i Island	Protects last surviving plant of *Hibiscadelphus crucibracteatus* from axis deer	Initially effective, but plant appears dead as of 1/85	P. Connally; R. Hobdy
Mo-1-DLNR-C-84-4-Kaunakakai (SE)	Protect several hundred individuals of the very rare *Sesbania arborea* from axis deer and cattle	Not yet re-evaluated	Established by DLNR-DOFAW (Wailuku) with permission of Hawaii Home Lands Commission
Gardenia 0-1-DLNR/private-(Honolulu) C-35-0.004	Protects a single plant of *Gardenia brighamii* in pasture of private ranchland	Tree still survives, but no reproduction	DLNR-DOFAW

Descriptor format: Island and volcanic mass/reference #, based on order of exclosure establishment in each location/agency responsible/vegetation zone of Ripperton and Hosaka, 1942/ last two digits of year established/size in hectares/USGS Quadrangle in which the exclosure is located.

Example:

EMa-4-DLNR-D3-76-Ø.2-Kaupo (NE) = East Maui, 4th exclosure established there, Hawai`i Department of Land and Natural Resources responsible, within Ripperton and Hosaka zone D3- open forest of *Acacia koa*, exclosure established in 1976, Ø.2 hectares in size, located within northeast quadrant of USGS Kaupo Quadrangle.

Descriptors:

Location--
- HMK - Island of Hawai`i, Mauna Kea
- HML - Island of Hawai`i, Mauna Loa
- HHu - Island of Hawai`i, Hualalai
- HKo - Island of Hawai`i, Kohala
- HKi - Island of Hawai`i, Kilauea
- EMa - Island of Maui, East Maui (Haleakala)
- WMa - Island of Maui, West Maui (West Maui Mtns.)
- Kah - Island of Kaho`olawe
- L - Island of Lana`i
- Mo - Island of Moloka`i
- O - Island of O`ahu

Agency--
- BE - Bishop Estate
- DLNR - Hawai`i Department of Land and Natural Resources
- DOFAW - Hawai`i Division of Forestry and Wildlife
- FS - Forest Service
- MKR - Mauna Kea Ranch
- NPS - National Park Service
- SCS - Soil Conservation Service
- TNC - The Nature Conservancy
- USN - U.S. Navy

Table 2. Simplified version of the Ripperton and Hosaka (1942) classification.[1]

Climatic Regime	Zone	Vegetation Class	Vegetation Association
Xerotropical (leeward lowland to submontane)	A	Savannah and dry grassland	Prosopis savannah and Heteropogon-Rhynchelytrum grassland
	B	Dryland sclerophyll forest (or scrub)	Metrosideros-Diospyros open forests; replacement vegetation: Leucaena scrub and forest
	C	Mixed mesophytic forest (woodland or scrub). C1 low phase, C2 high phase	Acacia koa open forests; replacement vegetation Psidium guajava, Eugenia cuminii forests or woodland
Pluviotropical (windward lowland to upper montane)	D1	Lowland rain forest	Metrosideros forests
	D2	Montane rain forest	Metrosideros-Cibotium and dominantly Cibotium forests
	D3	Upper montane rain or cloud forest	Cheirodendron or Acacia koa-Metrosideros mixed forests

Climatic Regime	Zone	Vegetation Class	Vegetation Association
Cool tropical (upper montane to alpine); only on Maui and Hawai`i	E1	Mountain parkland and savannah	*Acacia koa*-*Sophora chrysophylla* tree communities, *Deschampsia* tussock grassland
	E2	Subalpine forest and scrub	*Sophora*-*Myoporum* tree communities, *Styphelia*-*Vaccinium*-*Dodonaea* scrub communities
	E3	Sparse alpine scrub	*Styphelia*, *Vaccinium* and moss desert *Rhacomitrium lanuginosum* var. *pruinosum*

1 Scheme for zonal vegetation in Hawai`i adapted from Mueller-Dombois and Gagne in Wagner, Herbst, and Yee (this volume).

in physical, chemical, and biotic characteristics of the soil; changes in associated fauna, etc. Exclosures built for this purpose show tremendous differences in recovery potential, related mainly to ecosystem type, degree of animal damage, and presence of one or more highly competitive exotic plant species. These exclosures also satisfy the first objective.

Provide Ungulate-free Areas for Biological Experiments

This objective has been used infrequently in Hawai'i. Scowcroft (1981) successfully used HMK-6 to determine if recovery of mamane (*Sophora chrysophylla*) forest could be enhanced by direct sowing of mamane seeds. Skolmen (1978) used a pig- and cattle-proof exclosure (HMK-14) to study survival, growth, and disease susceptibility of vegetatively-grown koa (*Acacia koa*) progeny.

Preserve Populations of One or More Rare Plant Species or Small Tracts of a Rare Plant Community Which Would Otherwise be Lost through Animal Damage

Several exclosures have been erected in the past few years primarily to protect localized populations of single species. Target species have included *Argyroxiphium sandwicense* subsp. *sandwicense*, *Remya mauiensis*, *Sesbania arborea*, *Pittosporum confertiflorum*, and *Platanthera holochila*. In each case the projects have been emergency efforts to save populations before they are extirpated. It is too early to say how successful these projects will be in protecting naturally reproducing populations over the long term, but most would appear to have been highly successful in the short run in preventing what appeared to be certain extirpation of the populations. In exclosure HMK-6, results of Mauna Kea silversword plantings appeared promising with some apparent natural regeneration as of 2/83 (LLL). The rare *Dubautia arborea* was observed to be thriving in this same exclosure.

ASSESSING VEGETATION CHANGE

A variety of methods and sampling intervals has been used for assessing vegetation change in Hawaiian exclosures. Parameters of interest have been plant cover, density, survival, and growth. No one has reported studying changes in phytomass, although we see merit in such an approach.

Cover

Mueller-Dombois and Spatz (1975), Jacobi (1981), Katahira (1980), Mueller-Dombois (1981), and Scowcroft and Hobdy (in prep.) and others have used a point-frequency sampling method for estimating percentage ground cover and species composition. The method has 2 basic variants. For herbaceous vegetation and other plants less than 0.5 m tall, one or more sharpened metal rods are lowered at predetermined sampling points. Species touched by the tip of the rod are tallied. The other variant is applicable to trees and tall shrubs and uses an optical device which enables the observer to superimpose a single crosshair or a grid on the reflected image of the overhead vegetation. The theory and limitations of the point-frequency method are discussed more fully by Mueller-Dombois and Ellenberg (1974).

Scowcroft and Giffin (1983) used the line-intercept method to estimate cover in exclosures located in sparse subalpine forest on Mauna Kea. The method is applicable where individual plants have compact, discrete canopies.

Loope, Medeiros, and Crivellone (in prep.) and Loope, Medeiros, and Gagne (in prep.) used a network of relocatable transects of 1 m^2 plots as a standard technique for vegetation monitoring in Haleakala National Park (HALE). Cover for each species was estimated to the nearest 5%. This method introduces an undesirable element of subjectivity through need for estimation and resultant possibility of observer bias. However, the advantages of allowing precise relocation and resampling of identical areas were judged to outweigh disadvantages. The method seems particularly useful for understanding plant community dynamics on a micro-scale and lends itself well to combination with photo-documentation of changes.

Mueller-Dombois and Spatz (1975) used permanent 10 m^2 plots and the releve method of Braun-Blanquet to estimate cover/abundance in HAVO.

Basal area has also been used as a measure of cover in Hawaiian exclosures (Scowcroft and Giffin 1983). The method involves measuring the diameter or circumference at ground-line of each individual in a sample plot. It is a tedious technique and applicable only to perennials in areas with sparse vegetation.

Density

The density of individuals of a given species has been determined inside and outside exclosures by systematically examining every square meter (Scowcroft and Hobdy, in prep.). The method is applicable to trees, single-stemmed annuals and perennials, bunch grasses, and tufted ferns, because individuals are easily recognized (Mueller-Dombois and Ellenberg 1974). Counting individuals in randomly located quadrats has been used to estimate density of tree reproduction (Skolmen and Fujii 1980). In most cases, however, the exclosures have been generally small enough to permit complete counts.

Survival and Growth

The measure-tag-remeasure method has been used in exclosure studies to determine survival and growth of tree reproduction for preferred browse species (Skolmen and Fujii 1980; Scowcroft and Giffin 1983).

Statistical Analysis

Statistical analyses of cover, abundance, and other exclosure data have rarely been used. Scowcroft and Giffin (1983) used the Bonferroni t-test to compare changes in basal area cover inside exclosures with that outside and to test the hypothesis that protected plants were not significantly taller than unprotected ones. Those same authors reported using a procedure described by Draper and Smith (1966) to determine if growth rates of protected koa seedlings differed among exclosure sites.

Statistical treatment of point-frequency data is possible, but the use of normal statistical methods requires that each sampling point be located randomly and independently of every other point. Stratified random sampling may be desirable. Uniformly spaced sample points along uniformly spaced line transects are a design more often used because of its simplicity. However, this design fails to meet the criteria of randomness and independence. Nevertheless, some statisticians hold that point frame data can be analyzed with t-tests to indicate the degree of difference between fenced and unfenced areas and before and after fencing. Scowcroft and Hobdy (in prep.) used the t-test to analyze point frame data from EMa-4.

We suggest researchers consider using multivariant statistical methods (Stroup and Stubbendieck 1983) to determine the effect of protection from grazing and browsing on species composition.

Sampling Frequency

Sampling has typically been done when the exclosure is built and annually thereafter for 1 to 5 years. More frequent sampling during the first year after fencing may be desirable where conditions for rapid growth prevail. Sampling prior to erection of the exclosure has rarely been done but can help in the planning stage to assess the degree of similarity of areas slated for protection and control.

Adequacy of Methods

We conclude that methods used have, in general, been adequate to accomplish objectives. The difficulty of identifying plant species, especially non-flowering grasses, seems the greatest potential source of error. Another problem can be failure to precisely relocate and resample transects, plots, and individual plants. Adequate, durable marking is necessary. Statistical analyses of the data are desirable and existing analytical methods are applicable. We recommend consultation with a statistician during the early design stages of a study. However, we also recognize that the response of preferred browse species to release from browsing may be so dramatic that statistics are superfluous.

SUMMARY OF VEGETATION RESPONSE IN HAWAIIAN EXCLOSURES

Exclosures constructed in the Hawaiian Islands to date have, without major exception, enclosed vegetation damaged by feral animals for the purpose of allowing, studying, and/or demonstrating recovery (objectives 1 and 2). Some of these same exclosures have satisfied objectives 3 and 4. The degree to which recovery has actually occurred has varied tremendously, even within comparable stands of vegetation. In light of this variability, we suggest that it is unwise to base management recommendations and decisions on the results from 1 or even 2 exclosures in a given situation, especially if the exclosures are small. Findings on one island should not be extrapolated to another island even though the ecosystems are comparable.

The following discussion of vegetation response in Hawaiian exclosures, organized by broad vegetation zones, is necessarily simplified but indicates trends. Those interested in more detail should consult the references or sources given in table 1.

Leeward Low/Middle Elevation Shrubland/Grassland (Corresponds to Zones A, B of Table 2)

Mueller-Dombois and Spatz (1975) and Mueller-Dombois (1979, 1981) have reported on 10 years of vegetation recovery under protection from goats in HAVO. Dramatic vegetation changes occurred following removal from foraging pressure, but most of these involved changes in the dominant aliens. The major exception was the endemic vine, *Canavalia kauensis*, which was not seen prior to goat removal. The population size of this legume has fluctuated inside exclosure HKi-1 since establishment, with cover values ranging from 46% to 2%. Mueller-Dombois (1981) attributed the fluctuations of *Canavalia* to synchronized, life cycle-dependent death of cohorts, a process which may occur independent of climatic fluctuations, phenology, or succession.

Leeward Low/Middle Elevation Forest (Zones B, C)

The Nature Conservancy (TNC) exclosure at Auwahi at 975-1,035 m elevation on East Maui's south slope

(EMa-2) was one of the few constructed in these forests. The site was chosen following a survey by Lennox (1967) for its high concentration of very rare trees (Ochrosia haleakalae, Pelea multiflora, Streblus (Pseudomorus) sandwicensis, Tetraplasandra meiandra, etc.). Kikuyugrass (Pennisetum clandestinum), an aggressive alien, was becoming established in the area at the time the exclosure was built and greatly increased its dominance in the first year following construction (C.G. Lennox, pers. comm.). Due to exclusion of grazing, kikuyugrass became even denser inside the exclosure than out, preventing any seedling establishment and eventually leading to abandonment of the project.

More recently constructed exclosures within HALE (EMa-5, -14), located at the upper elevational limits of this forest zone, have shown modest success in reproduction of some native species, but mainly the more common ones (Loope, Medeiros, and Crivellone, in prep.). Reproduction of common native trees in the lowland zone of HAVO following goat removal has been good (Williams 1980). In general, it is clear that displacement by introduced grasses and forbs poses a major problem for reproduction of leeward native tree species of Hawai'i. Other problems may exist as well, including predation on seeds by rodents, loss of pollinators, changes in microclimate due to forest destruction, etc. (Medeiros, Loope, and Holt, in prep.).

Acacia koa Forest (Zones C, D, E1)

This vegetation type can be separated into montane koa parkland and moist koa and koa-'ohi'a forests. Two feral goat exclosures exist in koa parkland. Data from EMa-4 showed that when goat browsing was eliminated, koa and other native woody reproduction became established and grew rapidly (Scowcroft and Hobdy, in prep.). No such reproduction was observed outside the fenced area. Molassesgrass (Melinus minutiflora) became the dominant ground cover inside EMa-4. In HAVO, results from HML-1 showed that goat browsing pressure stimulated root suckering but suppressed sucker growth (Spatz and Mueller-Dombois 1973). Following goat control in that area in the mid-1970's, koa has reproduced well both by seed and vegetatively.

Data from a cattle exclosure in a moist koa-'ohi'a forest (HML-2) showed that elimination of cattle alone results in the establishment of koa seedling regeneration sufficient to restock the area (Skolmen and Fujii 1980). Scarifying the soil surface greatly enhances seedling emergence and establishment. Reintroducing cattle before koa are tall and sturdy enough to resist being walked down results in severe browsing damage.

In another moist koa forest, the failure of planted koa seedlings inside a cattle- and pig-proof exclosure (HMK-14) indicated that competition with banana poka (Passiflora mollissima) and other plants rather than animal damage were inhibiting reestablishment of koa (R.G. Skolmen, pers. comm.).

Metrosideros Rain Forest (Zones D1, D2, D3)

Few exclosures have been built in this forest type. As a result, we know little about the impact of feral pigs on understory vegetation and ecosystem processes and we have little information about forest response to protection from feral pigs. Katahira (1980) found dramatic recovery of native vegetation in exclosure HKi-5 after 4.5 years. 'Ama'u fern (Sadleria pallida) increased from 4.9% to 47.8% cover; hapu'u (Cibotium spp.) increased from 1.0% to 6.0%; and Clermontia parviflora, initially absent, attained a 3.4% cover.

On the other hand, relatively modest changes in rain forest understory were found by Higashino and Stone (1982) in HKi-2 after 13 years and Loope, Medeiros, and Crivellone (in prep.) in EMa-8 after 4 years of protection from pigs.

Subalpine Forest/Shrubland (Zones E2, E3)

This forest type occurs only on Mauna Kea, Mauna Loa, Hualalai, and Haleakala, but most exclosures have been built on Mauna Kea and Haleakala. A series of exclosures built on Mauna Kea in the 1960's (HMK-2, -3, -4, -5) and the 1970's (HMK-6, -7, -8) clearly showed that feral sheep (Ovis aries) suppress reproduction of mamane and other native browse species (Scowcroft and Giffin 1983). Photos of HMK-4 showed that mature mamane trees inside stayed healthy and lost their browse-line, while many trees of comparable size outside died. Suppression of regeneration and the death of old mamane appear to account for the gradual thinning of the forest in the vicinity of HMK-3 and HMK-7 (Scowcroft 1983). Judging from the mamane recovery inside the exclosures, we suspect that in the absence of browsing the ecosystem will recover with little help from land managers. Monitoring is needed to assess recovery and show managers where reforestation efforts are needed.

Results from the Honokahua exclosure (EMa-1) in Haleakala Crater are not as encouraging. Jacobi (1980) found no mamane seedling reproduction after 11 years of protection from goats, despite the presence and continued production of viable seed and the occasional emergence of seedlings. He hypothesized that because harsh environmental conditions inhibited seedling establishment, vegetative regeneration was the more important mechanism for maintaining the species in this habitat. Data from outside the exclosure indicated that only 50% of the dead mamane still had basal sprouts capable of replacing the parent tree if released from goat browsing.

Preliminary results after 3 years from the Pu'u Mamane exclosure (EMa-11) in Haleakala Crater showed good vegetative recovery of mamane and *Dubautia menziesii*, but no recruitment of seedlings. Mamane seedlings are not uncommon within the exclosure, but grow very slowly and have high mortality rates. Competition with the introduced grass *Holcus lanatus* appears to be a major deterrent to germination, growth, and survival of mamane seedlings (Loope, Medeiros, and Crivellone, in prep.).

Subalpine Grassland (Zone E1)

The *Deschampsia australis*-dominated grasslands of Kalapawili Ridge on the north rim of Haleakala Crater are a unique vegetational feature in Hawai'i (Vogl and Henrickson 1971). A survey in 1973 showed that damage by feral pigs had resulted in exposure of 23% bare ground and 18% cover of alien species (mainly *Holcus lanatus* and *Hypochaeris radicata*; Jacobi 1976, 1981). A small exclosure (EMa-3) was constructed in 1974 to determine the potential of the native *Deschampsia* vegetation to survive and/or recover in the absence of pig digging (Jacobi 1976). Sampling at intervals since (most recently in 6/83) showed that the native grass holds its own against the aliens in the absence of further disturbance (Jacobi 1981, pers. comm.).

Montane Bogs (Azonal)

East Maui's high elevation bogs occur as small habitat islands surrounded by rain forest or (in one case) grassland. These and other Hawaiian bogs contain a unique assemblage of endemic plant species derived from ancestors in bogs, wet forests, and alpine habitats in Hawai'i and elsewhere in the world (Loope, Medeiros, and Gagne, in prep.). Damage to East Maui high elevation bog vegetation by rooting of feral pigs has become severe in the past decade and has prompted fencing of 3 bogs in HALE. In Flattop Bog (EMa-7), 2 aggressive alien species (*Holcus lanatus*, *Hypochoeris radicata*), which were well established prior to fencing, increased substantially during the 4 years following fencing, occupying bare ground exposed by pig digging and displacing some of the native vegetation. In Greensword Bog (EMa-12), where these introduced plants were not established prior to fencing, the cover of the endemic sedges *Oreobolus furcatus* and *Carex svenonis* increased from 5% to 40% in 2 years after fencing. Although much bare ground remained after 2 years, the native sedges appeared capable of reoccupying their former habitat through seedling establishment and vegetative growth. Failure of the aliens to establish in the bog after fencing suggests that their dispersal into a new area is very slow without the aid of feral pig movement.

"NATURAL EXCLOSURES" AND THEIR IMPLICATIONS

Feral animals have had an overwhelming, but not ubiquitous, influence on Hawaiian vegetation. As a result of some very steep topography, some areas have remained untouched by herbivores. Most of these areas are on cliff faces and provide only atypical samples of pristine Hawaiian vegetation, although they are important in allowing survival of certain vulnerable native species. A few kipukas surrounded by rough lava flows on Hawaii (Stone, pers. comm.) and a few gently-sloping areas have escaped the effects of feral animals as a result of adjacent steep topography, just as a few mesa tops of Zion National Park, Utah, have escaped livestock grazing (Madany and West, 1984). Such Hawaiian areas known to us include Oloku'i on Moloka'i and Lihau and Mt. 'Eke on West Maui. No one has yet published information on the vegetation of these sites, although some detailed vegetation data were gathered by the U.S. Fish and Wildlife Service Hawaii Forest Bird Survey in 1980 on Oloku'i. Observations by L.L. Loope, R. Hobdy, and A.C. Medeiros on Lihau and Mt. 'Eke suggest that the pristine vegetation of these undisturbed sites is essentially intact and introduced species are almost lacking. On these sites, there has been no displacement of native vegetation by introduced species. Although more rigorous evaluation is clearly needed, the conclusion that introduced flowering plant species require feral animals or direct human influence as a vector for significant displacement of native Hawaiian species appears warranted.

NEEDS FOR THE FUTURE

It appears to us that almost every exclosure in Hawai'i has served to demonstrate impacts of vertebrate herbivores (objective 1). We see no pressing need for establishment of additional exclosures solely for this purpose, although improved documentation in published ecological literature is desirable. Exclosures built to study recovery potential (objective 2) will automatically demonstrate the impacts of vertebrate herbivores. Determination of recovery potential is being fairly well achieved in subalpine forest/shrubland, but is not being met in most other ecosystems due to small sample size and variability of local conditions. Establishment of additional exclosures appears most urgently needed in leeward mid- and low-elevation areas to gain a better understanding of possibilities for preserving representative tracts of this quickly disappearing vegetation in carefully chosen areas (e.g., Medeiros, Loope, and Holt, in prep.). Small exclosures appear satisfactory for predicting vegetation recovery over large areas, provided enough are built to sample the range of habitat conditions. Continued maintenance and monitoring of existing exclosures are as important as establishment of even urgently needed new ones.

Continued and expanded use of exclosures to test experimental manipulation as a management tool in the absence of alien herbivores (objective 3) shows promise. One useful application involves experimental control of alien species within exclosures to determine whether certain native plant species can reproduce when potential "safe sites" (Harper 1977) for seedling establishment are released from dominance by these aliens. Another application involves testing hypotheses about population dynamics and plant succession in koa-'ohi'a forests.

We have difficulty making predictions regarding the future role or success of exclosures in the protection of rare plant species (objective 4). We suspect that as the native Hawaiian flora continues to dwindle (see Wagner, Herbst, and Yee, this volume), what is left will be perceived as more valuable, and pressures will arise to do what is possible to save dwindling populations. Fencing, in spite of its very serious limitations and often prohibitive costs, seems to provide the only immediate hope for saving populations and communities impacted by feral or domestic ungulates. We suggest that such projects be well thought out and based on the best available information (usually from results of exclosure studies in comparable situations) to assure that the best sites are protected and at least a moderate chance of success exists. An accumulation of failures will undoubtedly lead to loss of enthusiasm, followed by loss of moral and financial support.

Experience (especially that from "natural exclosures") indicates that the sooner alien ungulates are removed from Hawai'i's wildlands, the greater the likelihood of ecosystem recovery. The more a site has been degraded by feral animals, the less the chance of success. The chance for recovery also becomes smaller as the extent of degradation becomes greater. With these thoughts in mind, we recommend that action to protect Haleakala's Kipahulu Valley from feral pigs be taken as soon as possible if it is to be taken at all. We also caution that recovery potential of a certain ecosystem type demonstrated within an exclosure today may be greatly reduced after years of continuing damage by alien ungulates.

Finally, we recommend that comprehensive monitoring be carried out to document biotic and physical changes resulting from large fencing projects in national parks and other sites for purposes of preservation of native biota and watershed protection. A firm scientific basis will be necessary to objectively evaluate the benefits in relation to costs of such endeavors.

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LITERATURE CITED

Baker, J.K., and D.W. Reeser. 1972. Goat management problems in Hawaii Volcanoes National Park: a history, analysis, and management plan. Natl. Park Serv. Nat. Resour. Rep. 2.

Coblentz, B.E. 1977. Some range relationships of feral goats on Santa Catalina Island, California. J. Range Manage. 30:415-419.

Draper, N.R., and H. Smith. 1966. Applied regression analysis. New York: John Wiley Sons, Inc.

Harper, J.L. 1977. Population biology of plants. New York: Academic Pr.

Higashino, P.K., and C.P. Stone. 1982. The Fern Jungle exclosure in Hawaii Volcanoes National Park: thirteen years without feral pigs in a rain forest. [Abstract] Proc. 4th Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 86. Honolulu: Univ. Hawaii.

Jacobi, J.D. 1976. The influence of feral pigs on a native alpine grassland in Haleakala National Park. Proc. 1st Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 107-112. Honolulu: Univ. Hawaii.

Jacobi, J.D. 1980. Problems with the long-term maintenance of mamane (Sophora chrysophylla) in the central crater area of Haleakala National Park. Proc. 3rd Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 167-171. Honolulu: Univ. Hawaii.

Jacobi, J.D. 1981. Vegetation changes in a subalpine grassland in Hawaii following disturbance by feral pigs. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. 41. Honolulu: Univ. Hawaii.

Jane, G.T., and L.T. Pracy. 1974. Observations on two animal exclosures in Haurangi Forest over a period of twenty years (1951-1971). New Zealand J. For. 19:102-113.

Katahira, L. 1980. The effects of feral pigs on a montane rain forest in Hawaii Volcanoes National Park. Proc. 3rd Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 173-178. Honolulu: Univ. Hawaii.

Kightley, S.P.J., and R.I.L. Smith. 1978. The influence of reindeer on the vegetation of South Georgia: I. Long term effects of unrestricted grazing and the establishment of exclosure experiments in various plant communities. Brit. Antarct. Surv. Bull. 44:57-76.

Lennox, C.G. 1967. Auwahi forest survey report. The Nature Conservancy, Honolulu. Typescript.

Lock, J.M. 1977. Preliminary results from fire and elephant exclusion plots in Kabalega National Park, Uganda. East Africa Wildl. J. 15:229-232.

Loope, L.L., A.C. Medeiros, and C.F. Crivellone. In prep. A review of results of exclosure studies in Haleakala National Park and vicinity. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. Honolulu: Univ. Hawaii.

Loope, L.L., A.C. Medeiros, and B.H. Gagne. In prep. Montane bogs of East Maui. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. Honolulu: Univ. Hawaii.

Madany, M.H., and N.E. West. 1984. Vegetation of several relict mesas in Zion National Park. J. Range Manage. 37(5):456-461.

Marquis, D.A. 1974. The impact of deer browsing on Allegheny hardwood regeneration. U.S. For. Serv. Res. Pap. NE-308. Upper Darby, Penn.: Northeast. For. Exp. Stn.

Medeiros, A.C., L.L. Loope, and R.A. Holt. In prep. Status of native flowering plant species on the south slope of Haleakala, East Maui. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. Honolulu: Univ. Hawaii.

Mueller-Dombois, D. 1979. Succession following goat removal in Hawaii Volcanoes National Park. Proc. 1st Conf. Sci. Res. Natl. Parks, 2:1149-1154. Washington, D.C.: Govt. Print. Off.

Mueller-Dombois, D. 1981. Vegetation dynamics in a coastal grassland of Hawaii. Vegetatio 46:131-140.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. New York: John Wiley Sons, Inc.

Mueller-Dombois, D., and G. Spatz. 1975. The influence of feral goats on the lowland vegetation in Hawaii Volcanoes National Park. Phytocoenologia 3:1-29.

Ripperton, J.C., and E.Y. Hosaka. 1942. Vegetation zones of Hawaii. Hawaii Agric. Exp. Stn. Bull. 89.

St. John, H. 1972. Canavalia kauensis (Leguminosae), a new species from the island of Hawaii. Pac. Sci. 26:309-414.

Scowcroft, P.G. 1981. Regeneration of mamane: effects of seedcoat treatment and sowing depth. For. Sci. 27:771-779.

Scowcroft, P.G. 1983. Tree cover changes in mamane (*Sophora chrysophylla*) forests grazed by sheep and cattle. Pac. Sci. 37:109-119.

Scowcroft, P.G., and J. Giffin. 1983. Feral herbivores suppress mamane and other browse species on Mauna Kea, Hawaii. J. Range Manage. 36:638-645.

Scowcroft, P.G., and R. Hobdy. In prep. Recovery of montane koa parkland vegetation protected from feral goats. U.S. For. Serv., Honolulu.

Skolmen, R.G. 1978. Vegetative propagation of *Acacia koa* Gray. Proc. 2nd Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 260-273. Honolulu: Univ. Hawaii.

Skolmen, R.G., and D.M. Fujii. 1980. Growth and development of a pure stand of koa (*Acacia koa*) at Keauhou- Kilauea. Proc. 3rd Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 301-310. Honolulu: Univ. Hawaii.

Spatz, G., and D. Mueller-Dombois. 1973. The influence of feral goats on koa tree reproduction in Hawaii Volcanoes National Park. Ecology 54:870-876.

Stroup, W. W., and J. Stubbendieck. 1983. Multivariate statistical methods to determine changes in botanical composition. J. Range Manage. 36:208-212.

Tiedemann, A.R., and H.W. Berndt. 1972. Vegetation and soils of a 30-year deer and elk exclosure in central Washington. Northwest Sci. 46:59-66.

Vogl, R.J., and J. Henrickson. 1971. Vegetation of an alpine bog on East Maui, Hawaii. Pac. Sci. 25(4): 475-483.

Wagner, W. L., D.R. Herbst, and R. S. N. Yee. Status of the native flowering plants of the Hawaiian Islands. [This volume]

Williams, J. 1980. Native vs. exotic woody vegetation recovery following goat removal in the eastern coastal lowlands of Hawaii Volcanoes National Park. Proc. 3rd Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 373-382. Honolulu: Univ. Hawaii.

13.

'OHI'A DIEBACK AND PROTECTION MANAGEMENT OF THE HAWAIIAN RAIN FOREST

Dieter Mueller-Dombois

ABSTRACT

The facts about the 'ohi'a (Metrosideros polymorpha) rain forest dieback are put together in abbreviated form as far as they have been revealed over the past 12 years of intensive research in Hawai'i. They lead to the conclusion that this native rain forest ecosystem is made up of an irregular and dynamic mosaic of 'ohi'a cohort stands occurring side by side. These are in different and similar life stages and successional development. Unlike a multi-species forest with steady-state stand segments, the Hawaiian rain forest appears to break down periodically in larger and smaller stand segments. The primary cause of this breakdown or canopy dieback is considered to be cohort senescence rather than biotic diseases or abiotic environmental fluctuations. The last 2 disturbances are believed to act at secondary levels. The original mosaic, however, is suggested to be largely the result of catastrophic disturbances, which recur rather infrequently on the same site. Recovery following dieback depends largely on the underlying soil-substrate mosaic and the associated species. On nutritionally poor sites, 'ohi'a sapling cohorts following dieback have a better chance of developing a second canopy than on nutritionally rich sites where competition of other species is strong.

This new knowledge has important implications for protection management, particularly with regard to the design of Hawaiian rain forest preserves. For this, ecosystem criteria referring to the considerations of vegetation dynamics given here and the knowledge gained from a one-time survey of current native forest bird refugia by the U.S. Fish and Wildlife Service should be combined. A number of specific management-related research tasks are suggested, such as mapping an already established physical and chemical habitat classification (at 1:24,000) and superimposing on it the

forest vegetation according to structural and compositional criteria in terms of stand life-stage and canopy vigor. A new strategy for alien species control involving soil-site fertility and dieback criteria is suggested for testing. Further monitoring of an established network of permanent plots and experimental sites is considered a continuing source for management-related information.

INTRODUCTION

When driving along the major access routes through the Hawaiian rain forest, one notices 'ohi'a (*Metrosideros polymorpha*) tree stands in different stages of vigor and stand condition. Some stands are dense with closed canopies, others contain trees with stag-headed (= dead) crowns and leafy branches along their trunks. Some stands consist of scattered 'ohi'a trees with dense treefern (*Cibotium* spp.) undergrowth, others of mostly dead 'ohi'a trees, while still others are green and healthy looking.

In the early 1970's, the dead and dying 'ohi'a stands were widely thought to be infected by a new and deadly disease (Burgan and Nelson 1972). A prediction was made (Petteys, Burgan, and Nelson 1975) that the entire 'ohi'a forest would soon succumb to this disease. An estimate for the extinction time was given as 15 to 25 years. The estimate was based on an analysis of 3 successively taken sets of aerial photographs (dated 1954, 1965 and 1972) and covering a territory of 80,000 ha on the windward slopes of Mauna Kea and Mauna Loa on the island of Hawai'i.

At the end of almost a decade of intensive disease and insect pest research involving many experts, it was concluded that the 'ohi'a "decline" or "dieback" was not caused directly by any of the discovered biotic disease or pest agents (Papp et al. 1979). Instead, it was considered to be caused by a combination of factors involving abiotic, environmental disturbances or stresses together with biotic agents, with the last playing a secondary role (Hawai'i Department of Land and Natural Resources 1981).

FIVE FACTS FROM VEGETATION RESEARCH

Research on soils and 'ohi'a tree populations throughout the 80,000 ha terrain on the island of Hawai'i was begun in 1975, first by a team consisting of myself and several of my graduate students (Mueller-Dombois et al. 1977, 1980) and then also by the U.S. Forest Service (Adee and Wood 1981). A number of facts were discovered. The most outstanding of these were:

1. That in many cases, 'ohi'a dieback was associated with 'ohi'a reproduction.

2. That the 'ohi'a dieback in each situation sampled was largely restricted to the canopy trees.

3. That the so-called "healthy" stands had usually no 'ohi'a saplings in their undergrowth.

4. That dieback stands were often sharply delineated from non-dieback stands along lava-flow boundaries.

5. That stand-level dieback occurred over the whole spectrum of soil substrates; that is, stands were dead or dying on relatively young and old lava flows; on pahoehoe and 'a'a lava; on well-drained and poorly-drained sites; on deep soils from volcanic ash; and also in young (200 years), recent (1,000 years) and old (over 5,000 years) soils and on permanently water-soaked, boggy soils.

'OHI'A DIEBACK SHOWS DIFFERENT PATTERNS AND SITE RELATIONSHIPS

We soon discovered that dieback was differently manifested over this site spectrum, and we distinguished 5 forms of stand-level dieback. These we called (Mueller-Dombois 1980, 1981):

1. Wetland dieback
2. Dryland dieback
3. 'Ohi'a displacement dieback
4. Bog-formation dieback
5. Gap-formation dieback.

Both wetland and dryland diebacks refer to 'ohi'a stands dying on lava flows or histosols with soil less than 50 cm deep over lava rock outcrop. The difference is that wetland dieback is associated with poorly-drained and dryland with well-drained substrates. Wetland dieback is more area-extensive, while dryland dieback is currently more restricted. Both forms of dieback are associated with 'ohi'a reproduction, that is, they are "replacement diebacks".

'Ohi'a displacement dieback occurs typically on deep soils from nutritionally rich (= eutrophic) ash, where 'ohi'a sapling development is suppressed (= quantitatively "displaced") by the dense growth of treeferns (Burton and Mueller-Dombois 1984).

Bog-formation dieback occurs also on deep soils from volcanic ash, but on those that are totally and permanently waterlogged. For a general distribution of these sites and dieback types, see Jacobi, Gerrish, and Mueller-Dombois 1983. In the bog-formation dieback, 'ohi'a reproduction appears to be mostly vegetative, often patchy, and of poor growth.

Gap-formation dieback was originally discovered on the knolls, ridges and slopes rising out of the boggy terrain (northwest of Hilo), where koa (Acacia koa) is sometimes a canopy associate of 'ohi'a (Mueller-Dombois 1981). The term gap-formation dieback refers to small stands dying in patches, where the trees lose their leaves without obvious physical damage to their branch system (like deciduous trees out of season). This feature applies to all 5 types of canopy dieback, but gap-formation dieback typically occurs on well- to moderately well-drained soils from ash (> 50 cm deep) that are not eutrophic, but rather nutritionally poor (= oligotrophic) or intermediate (= mesotrophic). 'Ohi'a reproduction is usually evident in such dieback stands, but undergrowth competition may lead to displacement in some cases.

The U.S. Forest Service vegetation and soil study team, directed by Ken Adee (Adee 1980, Adee and Wood 1981), came to very similar conclusions and discovered independently almost the same 5 dieback types, but Adee and Wood gave them somewhat different names (Hawai'i Department of Land and Natural Resources 1981). For example, they recognized a "pubescent structural dieback" type on well-drained soils, which we included in our dryland dieback type. Dieback stands on well-drained soils are indeed often of the pubescent-leaved varieties (M. polymorpha var. polymorpha or var. incana) but also include glabrous forms of 'ohi'a belonging to the varieties glaberrima and/or macrophylla.

During our initial field research, we noticed that in some places dominantly pubescent-leaved 'ohi'a stands seemed to be dying, while the upcoming saplings were dominantly glabrous forms. This led to the hypothesis of successional ecotypes, which we proposed for future study in our first synthesis report (Mueller-Dombois et al. 1977). Another idea put forth in that report was that the 'ohi'a rain forest in Hawai'i may consist of stands in different life phases, and we proposed the hypothesis of a forest life cycle, which I will refer to again.

ALTERNATE CAUSE HYPOTHESES

In the initial proposal to the National Park Service for dieback research, which resulted in the needed money in 1975 to do the first basic ecological fieldwork, I proposed as an alternative to the disease hypothesis that the dieback may be "a normal phenomenon, a developmental stage in the primary succession of an isolated rainforest ecosystem" (Mueller-Dombois 1974: 10). This natural-cause hypothesis was based on prior fieldwork (Mueller-Dombois and Krajina 1968) and a literature survey, which revealed that stand-level dieback in the Hawaiian Islands, particularly in its rain forests, had been noted and discussed by a number of authors (including Clarke 1875; Miller 1900; Lyon 1909, 1918, 1919; Curran 1911; Selling 1948; Fosberg 1972) prior to the discovery of dieback in the early 1970's.

At the conclusion of our basic ecological field survey (Mueller-Dombois et al. 1980), I proposed a new consolidated cause hypothesis for future research on the etiology of the Hawaiian rain forest dieback with the following words: It seems likely "that the dieback is initiated by a climatic instability which becomes effective through the soil moisture regime under certain conditions of forest stand maturity" (Mueller-Dombois 1980:159).

Since then a number of new facts have been accumulated which I can now put together under the 3 points raised in this more recent causal hypothesis.

PUTTING THE FACTS TOGETHER

Climatic Instability Factors

Doty (1982) and Evenson (1983) both studied long-term precipitation records in relation to dieback and independently came to the same conclusion that the year-to-year fluctuations in rainfall bear no clear relationship to 'ohi'a dieback. In an elaboration of the above-stated hypothesis, I suggested (Mueller-Dombois 1980:160) that a sequence of years wetter than normal may result in the drowning of root systems of 'ohi'a stands on poorly-drained sites, and that particularly dry periods may kill stands on well-drained sites. This part of the hypothesis now seems less probable. Moreover, Jacobi (1983) in his air-photo analysis of a 1,600 ha area near the 1,220 m level at the Saddle Road found that the wetland dieback progressed there particularly from 1965 to 1977, when rainfall was excessive only in 1969 and then remained below normal for several years in a row (from 1970 to 1975).

Two other important studies were done by the U.S. Forest Service. For 2 years, Doty (1980) monitored water-table fluctuations in adjacent dieback and non-dieback stands in the Waiakea Forest Reserve. He recorded considerable water-table fluctuations in relation to rain showers, but the water-table fluctuations were of similar magnitude in dieback and non-dieback stands, and non-dieback (or "healthy") stands did not become dieback stands when their root systems were temporarily flooded. Doty (1983) also analyzed stream flow data of the Wailuku River, which flows out of the dieback-affected Hilo watershed. He ascertained that rainfall variations were well reflected in the streamflow but that the dieback events had no effect on either volume of water or its sediment load and nutrient composition. He explained this with reference to the vegetation research, in which it was found that only the trees were dying while the undergrowth remained stable.

Soil Factors

Even if climatic stresses are involved, they alone can hardly account for the 'ohi'a dieback because of the discontinuous distribution of the dieback stands. Since these stands are often delimited by soil-substrate boundaries, one could think of soil as an important factor.

Kliejunas and Ko's (1974) experiment on fertilizing half-dead 'ohi'a gave strong evidence that nitrogen deficiency plays a role in the dieback syndrome. Since that time, we have completed our soil-nutrient and foliar analyses in relation to the broad spectrum of habitat and dieback types (Balakrishnan and Mueller-Dombois 1983). We found that young volcanic substrates (ash as well as pahoehoe) are particularly deficient in nitrogen; further, that the deep and organically enriched ash soils (about 1,000 years old) of Ola'a Tract are indeed nutritionally rich (= eutrophic), and that the older (over 5,000 years old) substrates exhibit poor nutrient balances, particularly on account of low phosphorus and potentially toxic levels of aluminum, manganese, and iron. Poor drainage and low pH further aggravate metal toxicity. Such soils would not be suitable for crop plants or for nutrient-demanding tree species, and plant nutrient stress is a characteristic of almost all 'ohi'a rain forest sites except the intermediately aged (about 1,000 years old) ash soils.

When we repeated Kliejunas and Ko's (1974) fertilizer experiment in a series of tall-statured dieback stands (Gerrish and Bridges 1984), we found that some dying trees could be revived as measured by diameter increments, but that their crowns did not gain any significant leaf biomass. This placed more emphasis on the third point raised in the 1980 cause-hypothesis, namely on the "certain stage of forest stand maturity", that is, on the life stage of the affected stands.

Stand Factors

Early on we recognized that only the canopy trees of 'ohi'a were dying, while the undergrowth seemed unaffected. This observation argued strongly against the idea of a new killer disease, and also against any violent physical damage (such as feral animals or fire) or severe physiological disturbance (such as air pollution or climatic change) as the cause. That the undergrowth remains stable during canopy dieback or may even increase in vigor, was indirectly determined also through Doty's (1983) watershed analysis. By not limiting our field research to dieback stands, but including many non-dieback or "healthy" stands in 'ohi'a population samples, we found that the so-called "healthy" stands usually consist of only 2 life-stages of 'ohi'a: mature trees and a scattering of small seedlings on decaying logs. In contrast, dieback stands consisted usually of at least 4 life stages: dieback trees, survivors, seedlings, and, in older dieback stands especially, 'ohi'a saplings. 'Ohi'a saplings often form dense stands, particularly in wetland and dryland dieback areas and along many rights-of-way, even on infrequently driven jeep roads. This is true regardless of location through dieback or non-dieback stands.

A recent reanalysis, after 5 years, of 26 of our permanent plots in dieback stands (Jacobi, Gerrish, and Mueller-Dombois 1983) gave further evidence that 'ohi'a reproduction, in any specific site or stand, occurs in "waves" or restricted periods rather than continuously. Only a disturbance, such as cutting down a stand for a right-of-way or the loss of canopy due to dieback, seems to set the stage for a new 'ohi'a sapling stand to become established. Such a sapling stand when growing on a given site can be called a <u>cohort</u>. The term cohort refers to individuals of the same species or variety when such individuals are members of the same generation occurring together in the same community. Cohort stands can be in different stages of development, such as juvenescence, adolescence, maturity, and late maturity or senescence.

Our earlier finding that dieback stands are often delimited from non-dieback stands along lava-flow boundaries, made us believe that soil is an important factor. But we have since found many dieback stands that are separated from non-dieback stands by no such soil boundaries. A good example is Jacobi's (1983) air photo analysis, where a wetland dieback on poorly drained pahoehoe progressed to an 'a'a flow and then stopped, but where it also stopped in the middle of the same pahoehoe flow and then did not progress after 1977.

Lava flow boundaries are not only physical soil boundaries. They are also historical boundaries, and the 'ohi'a stand analyzed by Jacobi (1983), which continued to die progressively from 1965 to 1977 across the poorly drained pahoehoe, was most probably in a senescing life stage. It bordered another 'ohi'a stand in a more vigorous life stage growing on the 'a'a lava, but it bordered also a still rather vigorous 'ohi'a stand on the same poorly drained pahoehoe.

From a synthesis of all the facts so far established, the cohort senescence theory was born (Mueller-Dombois 1982a, 1983a, 1983b, 1983c; Mueller-Dombois et al. 1983), and it serves currently as the most plausible explanation of 'ohi'a dieback.

APPLICATION TO MANAGEMENT

A New Viewpoint

When the previous "biological evaluation of the 'ohi'a decline" (Hawai'i Department of Land and Natural Resources 1981) was prepared as a guide to Hawaiian rain forest management by the U.S. Forest Service San Francisco Pest Management Unit, dieback was still viewed as a disease. However, there has been so far no evidence that 'ohi'a as a species has become subject to a disease of either biotic or abiotic origin, nor to a combination of the two. A disease is usually defined as a physiological or genetic abnormality occurring in an organism or population. Aging is clearly not a disease. It is part of life's program, and the dying of trees, particularly during late maturity or senescence, should not be considered abnormal.

What may strike one as abnormal is that such large tree stands are dying more or less in synchrony. However, we have now learned that the Hawaiian rain forest dieback is not entirely unusual. Similar forest stand diebacks occur also in other biomes, particularly where forests are dominated by one or a few canopy species (Sprugel 1976; Ash 1981; Stewart and Veblen 1982, 1983; Arentz 1983; Mueller-Dombois 1983d). Perhaps Hawai'i may be somewhat more extreme in this respect because of its geographic isolation and associated floristic history (Mueller-Dombois 1983c).

It is important to view the Hawaiian rain forest biome as an ecosystem with broader-scale spatial dynamics with regard to protection management than is usually understood from textbook information. The Hawaiian rain forest is not a climax forest in the conventional sense of Whittaker (1953), in which the canopy species are represented in any given forest stand by all age-classes and sizes or life-stages (such as seedlings, saplings, mature and senescing trees). Instead, sapling stands, mature-tree stands, and senescing stands are seen as occurring in a spatial side-by-side mosaic.

Design of Preserves

How did this spatial side-by-side mosaic originate? One thing is clear. The volcanic history has a lot to do with it on the island of Hawai'i. We witness there large stands of 'ohi'a, that is, cohort stands in different life-stages side by side on differently aged lava flows and ash deposits. Other large cohort stands may have originated from other catastrophic disturbances, such as hurricanes. On the older islands, smaller cohort stands of 'ohi'a are often associated with landslides (Mueller-Dombois 1982b). On the same site-location, catastrophic disturbances are very infrequent. Therefore, an 'ohi'a stand that originated from a catastrophic disturbance is not likely to be destroyed by a similar disturbance during its life time, unlike other forests, e.g. those with frequent fire-disturbance regimes. Thus, a (given) cohort stand in the Hawaiian rain forest usually has a chance to go from its mature life-stage to its senescing life-stage and to canopy dieback under natural conditions. Following that, there is usually a rebuilding of a new sapling stand as explained before, but this depends in part on the present site conditions and other factors, such as the presence of introduced species.

We know now that it is important for the design of ecological reserves in the Hawaiian rain forest biome to incorporate the cohort mosaic of 'ohi'a stands. For example, it does not appear sufficient to preserve a section of the 1942 lava flow, and to consider it an example of the Hawaiian rain forest. It is only an example, although in itself valuable, of a young life-stage of an 'ohi'a forest. Similarly, it is not sufficient to search for good and healthy looking mature 'ohi'a forests, such as occur in the crater-rim area of Hawai'i Volcanoes National Park or in Pu'u Maka'ala, and to set these aside believing they will remain healthy looking and good stand examples forever. In the next 50 or 100 years these good-looking closed-canopy forests may undergo dieback while other stands may mature. However, if other stands, perhaps now in dieback condition, have been subjected to "enrichment planting" with other species (as was suggested in the 1981 Hawai'i Department of Land and Natural Resources report) or if they have been converted to other uses, we will end up with preserves that represent only fragments of the Hawaiian rain forest biome.

Therefore, new management-oriented research is needed for the proper design of Hawaiian rain forest preserves, with ecosystem criteria based on 'ohi'a dieback research. In order of priority, research can be grouped into 3 work tasks: 1) Mapping of the physical habitat mosaic, which has now been established in the form of a simple and workable classification (Mueller-Dombois 1981; Balakrishnan and Mueller-Dombois 1983); 2) Mapping of 'ohi'a stands by stand condition and vigor state, which requires techniques already developed by Jacobi (1980, 1983); 3) The continuation of permanent plot studies (Jacobi, Gerrish, and Mueller-Dombois 1983) and longer-term research on our experimental sites (Gerrish and Bridges 1984). Tasks 1 and 2 can be applied from present knowledge as immediate work products for management decisions. Task 3 requires longer-term monitoring, which will yield increasing precision in predictive information for protection management.

Rare Endemic and Introduced Species

A number of rare endemic species are distributed throughout the 80,000 ha dieback and non-dieback territory across the eastern slopes of Mauna Kea and Mauna Loa (Mueller-Dombois et al. 1980). What happens to these species following canopy dieback has not yet been established. If species are shade-adapted, they may become locally extinct not only because of the increased exposure to light, but also because of the increased competition by heliophytes, such as the mat-forming native fern Dicranopteris linearis. Do these rare endemics return during canopy closure of the forest, or do they find refuge during the recovery process in the changing matrix of the dominant plant species?

One thing is clear already. Most native Hawaiian rain forest birds use non-dieback forests as refugia (Scott et al., in press) and seem to disappear from dieback stands. Do bird populations return when 'ohi'a cohort stands form closed canopies or regain maturity? And do they migrate in relation to their dynamic rain forest habitat? Such questions are important, if we want to find out how to manage the Hawaiian rain forest for the preservation of rare and endemic species. It is dangerous to use knowledge about bird refugia determined in one survey as a basis for permanent reserves. The reserves may collapse in the not too distant future while in the meantime other potential refugia have been given to other uses.

Senescing stands are a "weak" life-stage. Penetration by alien species during and after canopy dieback is a reality (Jacobi, Gerrish, and Mueller-Dombois 1983) in some cases, and a strong probability in others. Closed or "saturated" native communities are not as prone to alien species invasion as are dieback stands (Mueller-Dombois, Bridges, and Carson 1981). Of course, this depends in part on the life-form of the alien species. Feral pigs (Sus scrofa) may aggravate the effects of canopy dieback and thus aid in converting such stands into alien replacement communities. Little is known about this as yet. However, greater control efforts near dieback stands appear to be prudent (Mueller-Dombois et al. 1980), and the patterns of canopy dieback and recovery may be usefully incorporated into the strategies of protection management.

Soil Fertility

Because of Kliejunas and Ko's (1974) finding that inorganic nitrogen was involved in the 'ohi'a decline, it was suggested in the 1981 Hawai'i Department of Land and Natural Resources report that fertilizing dying 'ohi'a stands is a management option. Primarily because of the high costs of such undertaking, however, this option was not considered viable.

We can now say that fertilizing 'ohi'a dieback stands on an operational scale would probably be one of the worst mistakes in protection management. The reason for this is that dieback on infertile or nutritionally imbalanced soil-substrates guarantees a much better chance of 'ohi'a stand recovery than dieback on nutritionally improved or fertile sites. On fertile sites, we discovered the 'ohi'a displacement dieback. It comes about through the slow growth rates of 'ohi'a seedlings relative to those of the tree fern undergrowth (Burton and Mueller-Dombois 1984). The good 'ohi'a sapling recovery in the wetland and dryland diebacks is clearly a function of the high tolerance of 'ohi'a for nutritionally poor soils and the inhibited growth rate of competitors under such conditions. 'Ohi'a manages to achieve reasonable growth on such oligotrophic sites, while its competitors are kept in check. Moreover, oligotrophic habitats may be considered "natural exclosures" for many aggressive introduced plant species (Gerrish and Mueller-Dombois 1980). Most of the aggressive alien plants are adapted to nutritionally rich soils. They have a hard time competing with the tough and tolerant 'ohi'a on poor native soils in the montane rain forests of Hawai'i (Balakrishnan and Mueller-Dombois 1983).

The suggestion to map already classified physical habitats as a first priority management task, as stated before, would therefore serve at least 2 purposes: 1) the design of viable rain forest preserves, and 2) an improved strategy for alien species control.

Forest Hydrology

Doty's (1983) recent analysis of the Hilo watershed, in which large stands of 'ohi'a were subject to dieback, clearly shows that there is no need to replant trees in order to save the watershed. The native communities, in spite of obvious canopy disturbances, apparently stabilize the water flow primarily through their undergrowth.

Holt (1983) recently established, through historical file and literature research, that fear of losing the forest-watershed cover in connection with the "Maui Forest Trouble" caused a major replanting program with Australian tree species in the 1930's. However, in this case the sugarcane planters felt no need for this program in spite of the huge 'ohi'a dieback throughout their watershed. Their newly dug Maui ditch system was apparently operating just fine. It was Lyon (1918, 1919) who insisted on replanting with alien species, since he felt that the Hawaiian vegetation consisted primarily of pioneer species that could not adapt to changes such as toxification that come about with aging of tropical soils.

Similar ideas proved to have such a profound effect on forest watershed management in Hawai'i that some foresters believe that native tree species have to be replaced by introduced species. It will be necessary to put more management-related research efforts into finding out just how native species become adapted or decline in relation to soil aging and toxicity. It is of similar importance to find out in what way today's native rain forest vegetation has evolved from pioneer or colonizing ancestors. How far is successional adaptation developed or completed? Or is there a real difference between the isolated Hawaiian biomes and less isolated montane rain forest biomes elsewhere?

Apart from these fundamental questions, there is a real need for more pragmatic forest-hydrology research. Many foresters and biologists will probably agree that water and the native biota are the most important resources of the Hawaiian mountains. Their functioning and conservation management is very compatible with recreational and some forms of agricultural land use.

The U.S. Forest Service should play a more important role in forest hydrological research in Hawai'i. There is a real need to establish more sophisticated and multidisciplinary research on Hawaiian watersheds similar to research at Hubbard Brook and Coweeta in the eastern United States. There are at least 2 good reasons for having such studies in the State of Hawai'i: 1) Hawai'i supports the only large tropical montane rain forest in the United States. Results from Hawai'i are more applicable to other tropical areas than results from temperate forests. 2) Hawai'i can serve as a biological control for forests in the Atlantic region which are now impacted by new industrial stresses from air pollution (Smith 1981) and acid rain (Vogelman 1982; Ulrich 1982). Hawai'i could serve as a biological control for the biogeochemical cycling of nutrients in forest watersheds and the phenomenon of canopy dieback (Mueller-Dombois, Vitousek, and Bridges 1984) in more artificially stressed situations elsewhere.

CONCLUSIONS

Our 'ohi'a dieback research began with an ecological study of the problem as it presented itself during the 1970's. Since dieback did not turn out to be a new disease as most people had expected, agency support for further research was withdrawn. For this reason, we had to turn to the National Science Foundation (NSF) for further support. However, as a basic research supporting institution, NSF was not interested in management-oriented research. As a consequence we had to concentrate our efforts on fundamental research relating to the etiology of the Hawaiian forest canopy dieback and to the long-term ecosystem dynamics and development.

Questions raised in this paper under the section concerned with management application could not be included in our NSF-sponsored research. Therefore, clear-cut recommendations for specific management options or alternatives cannot be given here. Instead, a framework for new management related research is offered. This research should be carried out with agency funding (e.g. from the Hawai'i State Department of Land and Natural Resources, the U.S. Forest Service, the U.S. Fish and Wildlife Service, and the National Park Service).

In summary, management-related research tasks are here restated as:

1. The habitat types should be mapped on a large map scale, such as 1:24,000.
2. Cohort stands should be mapped according to stand condition and life stages on the same scale and superimposed on the physical habitat map.
3. This will form a basic tool for proper "minimal area" design of preserves from the viewpoint of ecosystem dynamics using plant ecological criteria.
4. These criteria should be integrated with those from the U.S. Fish and Wildlife Service Hawai'i Forest Bird Survey.
5. New studies should be initiated focusing specifically on the effect of dieback on rare endemic forest species.
6. New studies should be initiated focusing on the effect of dieback on alien species invasion.
7. Alien species control efforts should make use of and test the newly provided physical and chemical habitat classification once it is mapped (see item 1 above).
8. Monitoring vegetation changes in an established network of permanent plots (Jacobi, Gerrish, and Mueller-Dombois 1983) and experimental sites (Gerrish and Bridges 1984) should be continued.

In general, there is a need for a new view of the Hawaiin rain forest as an ecosystem composed of forest life stages which occur side by side in the form of an irregular mosaic. The Hawaiian rain forest should no longer be viewed as an ecosystem that is sick and doomed for extinction. In terms of watershed values, more confidence should be placed on the native vegetation as providing an inexpensive and functionally reliable plant cover. At the same time, there is an outstanding opportunity in Hawai'i for modern forest hydrological research to be done by the U.S. Forest Service as a service to the State, the Nation and the international community of tropical countries. Management efforts to preserve integrated units of the life-stage mosaic of the Hawaiian rain forest are definitely worthwhile. Such efforts should be incorporated as a high priority into Hawai'i Department of Land and Natural Resources management policy.

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LITERATURE CITED

Adee, K. 1980. Canopy structure in the ohia decline zone of Mauna Kea and Mauna Loa, Hawaii. [Abstract] Proc. 3rd Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 1. Honolulu: Univ. Hawaii.

Adee, K., and H. Wood. 1981. Regeneration and succession following canopy dieback in an ohia (Metrosideros polymorpha) rainforest on the island of Hawaii. U.S. For. Serv., Honolulu. Mimeo.

Arentz, F. 1983. Nothofagus dieback on Mt. Giluwe, Papua New Guinea. Pac. Sci. 37(4):453-458.

Ash, J.E. 1981. The Nothofagus Blume (Fagaceae) of New Guinea. In Biogeography and ecology of New Guinea, ed. G.L. Gressitt, Vol. 42, Biologicae, 355-363. The Hague, Netherlands: Dr. W. Junk Pub.

Balakrishnan, N., and D. Mueller-Dombois. 1983. Nutrient studies in relation to habitat types and canopy dieback in the montane rain forest ecosystem, island of Hawaii. Pac. Sci. 37(4):339-359.

Burgan, R. E. and R. E. Nelson. 1972. Decline of ohia lehua forests in Hawaii. U.S. For. Serv. Pac. Southwest For. Range Exp. Stn. Gen. Tech. Rep. PSW-3.

Burton, P.J., and D. Mueller-Dombois. 1984. Response of Metrosideros polymorpha seedlings to experimental canopy opening. Ecology 65(3):779-791.

Clarke, F.L. 1875. Decadence of Hawaiian forests. All about Hawaii (Thrum's Hawaiian Annual) 1:19-20. Honolulu: Thos. G. Thrum.

Curran, H.M. 1911. The Maui forests. Hawaii. For. Agric. 8:185-187.

Doty, R.D. 1980. Groundwater conditions in the ohia rain forest near Hilo. Proc. 3rd Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 101-111. Honolulu: Univ. Hawaii.

Doty, R.D. 1982. Annual precipitation on the island of Hawaii between 1890 and 1977. Pac. Sci. 36(4): 421-425.

Doty, R.D. 1983. Stream flow in relation to ohia forest decline on the island of Hawaii. Am. Water Resour. Assn. Water Resour. Bull. 19(2):217-221.

Evenson, W.E. 1983. Climate analysis in ohia dieback area on the island of Hawaii. Pac. Sci. 37(4): 375-384.

Fosberg, F.R. 1972. Guide to Excursion III. In Tenth Pacific Science Congress, rev. ed. Honolulu: Univ. Hawaii.

Gerrish, G., and K.W. Bridges. 1984. A thinning and fertilizing experiment in Metrosideros dieback stands in Hawaii. Hawaii Bot. Sci. Pap. 43.

Gerrish, G., and D. Mueller-Dombois. 1980. Behavior of native and non-native plants in two tropical rain forests on Oahu, Hawaiian Islands. Phytocoenologia 8(2):237-295.

Hawaii Department of Land and Natural Resources. 1981. A biological evaluation of ohia decline on the island of Hawaii. U.S. For. Serv., Pac. Southwest. Region, San Francisco Pest Manage. Unit and Hawaii Dep. Land Nat. Resour. Div. For. Wildl. Mimeo.

Holt, R.A. 1983. The Maui forest trouble: a literature review and proposal for research. Hawaii Bot. Sci. Pap. 42.

Jacobi, J.D. 1980. The vegetation map and legend. In Ohia rainforest study: ecological investigations of the ohia dieback problem in Hawaii, ed. D. Mueller-Dombois, J.D. Jacobi, R.G. Cooray, and N. Balakrishnan, 6-12. Hawaii Agric. Exp. Stn. Misc. Pub. 183.

Jacobi, J.D. 1983. Metrosideros dieback in Hawaii: a comparison of adjacent dieback and non-dieback rain forest stands. New Zealand J. Ecol. 6:79-97.

Jacobi, J.D., G. Gerrish, and D. Mueller-Dombois. 1983. Ohia dieback in Hawaii: vegetation changes in permanent plots. Pac. Sci. 37(4):327-337.

Kliejunas, J.T., and W.H. Ko. 1974. Deficiency of inorganic nutrients as a contributing factor to ohia decline. Phytopathology 64:891-896.

Lyon, H.L. 1909. The forest disease on Maui. Hawaii Planter's Rec. 1:151-159.

Lyon, H.L. 1918. The forests of Hawaii. Hawaii Planter's Rec. 20:276-281.

Lyon, H.L. 1919. Some observations on the forest problems of Hawaii. Hawaii Planter's Rec. 21:289-300.

Miller, L.H. 1900. Collecting trips. Verbatim copy of journal, the original of which was donated to Bancroft Library, Univ. Calif., Berkeley. Xeroxed copy in Sinclair Library, Univ. Hawaii.

Mueller-Dombois, D. 1974. The ohia dieback problem in Hawaii: a proposal for integrated research. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. 3. Honolulu: Univ. Hawaii.

Mueller-Dombois, D. 1980. The ohia dieback phenomenon in the Hawaiian rain forest. In The recovery process in damaged ecosystems, ed. J. Cairns, Jr., 153-161., Ann Arbor, Mich.: Ann Arbor Sci. Pub., Inc.

Mueller-Dombois, D. 1981. Spatial variation and succession in tropical island rain forests: a progress report. Hawaii Bot. Sci. Pap. 41.

Mueller-Dombois, D. 1982a. Canopy dieback in indigenous forests of Pacific Islands. Hawaii Bot. Soc. Newsl. 21:2-6.

Mueller-Dombois, D. 1982b. Island ecosystem stability and Metrosideros dieback. Proc. 4th Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 138-146. Honolulu: Univ. Hawaii.

Mueller-Dombois, D. 1983a. Canopy dieback and successional processes in Pacific forests. Pac. Sci. 37(4):317-325.

Mueller-Dombois, D. 1983b. Stand-level dieback in New Zealand forests and the theory of cohort senescence. Hawaii Bot. Soc. Newsl. 22:33-42.

Mueller-Dombois, D. 1983c. Population death in Hawaiian plant communities: a new causal theory and its successional significance. Tuexenia (Festschrift H. Ellenberg) 3:117-130.

Mueller-Dombois, D. 1983d. Canopy dieback and dynamic processes in Pacific forests: introductory statement and concluding synthesis. Pac. Sci. 37(4): 313-316, 483-488.

Mueller-Dombois, D., and V.J. Krajina. 1968. Comparison of east-flank vegetations on Mauna Loa and Mauna Kea, Hawaii. Rec. Adv. Trop. Ecol. 2:508-520.

Mueller-Dombois, D., K.W. Bridges, and H.L. Carson, eds. 1981. Island ecosystems: biological organization of selected Hawaiian communities. Stroudsburg, Penn.: Hutchinson Ross Pub. Co.

Mueller-Dombois, D., P.M. Vitousek, and K.W. Bridges. 1984. Canopy dieback and ecosystem processes in Pacific forests: a progress report and research proposal. Hawaii Bot. Sci. Pap. 44.

Mueller-Dombois, D., J.E. Canfield, R.A. Holt, and G.P. Buelow. 1983. Tree-group death in North American and Hawaiian forests: a pathological problem or a new problem for vegetation ecology? Phytocoenologia 11(1):117-137.

Mueller-Dombois, D., J.D. Jacobi, R.G. Cooray, and N. Balakrishnan. 1977. Ohia rain forest study: final report. Univ. Hawaii Coop. Natl. Park Resour. Stud. Unit Tech. Rep. 20. Honolulu: Univ. Hawaii.

Mueller-Dombois, D., J.D. Jacobi, R.G. Cooray, and N. Balakrishnan. 1980. Ohia rain forest study: ecological investigations of the ohia dieback problem in Hawaii. Hawaii Agric. Exp. Stn. Misc. Pub. 183.

Papp, R.P., J.T. Kliejunas, R.S. Smith, Jr. and R.F. Scharpf. 1979. Association of Plagithmysus bilineatus (Coleoptera: Cerambycidae) and Phytophthora cinnamomi with the decline of ohia-lehua forests on the island of Hawaii. For. Sci. 25: 187-196.

Petteys, E.Q.P., R.E. Burgan, and R.E. Nelson. 1975. Ohia forest decline: its spread and severity in Hawaii. U.S. For. Serv. Pac. Southwest For. Range Exp. Stn. Res. Pap. PSW-105.

Scott, J.M., S. Mountainspring, F.L. Ramsey, and C.B. Kepler. In press. Forest bird communities of the Hawaiian Islands: their dynamics, ecology, and conservation. Stud. Avian Biol.

Selling, O.H. 1948. Studies in Hawaiian pollen statistics. Part III. On the late Quarternary history of the Hawaiian vegetation. B.P. Bishop Mus. Spec. Pub. 39.

Smith, W.H. 1981. Air pollution and forests. Heidelberg, Berlin: Springer-Verlag.

Sprugel, D.G. 1976. Dynamic structure of wave-regenerated Abies balsamea forests in the northeastern United States. J. Ecol. 64:889-911.

Stewart, G.H., and T.T. Veblen. 1982. Regeneration patterns in southern rata (Metrosideros umbellata)-kamahi (Weinmannia racemosa) forest in central Westland. New Zealand J. Bot. 20:55-72.

Stewart, G.H. and T.T. Veblen. 1983. Forest instability and canopy tree mortality in Westland, New Zealand. Pac. Sci. 37(4):427-431.

Ulrich, B. 1982. Gefahren fur das Waldokosystem durch saure Niederschlage. In Sonderheft: Immissionsbelastungen von Waldokosystemen, 9-25. Landesanstalt fur Oekologie. Munster, Fed. Rep. Germany: Schutzgemeinschaft Deutscher Wald e.v., Landwirtschaftsverlag GmbH.

Vogelmann, H.W. 1982. Catastrophe on Camel's Hump. Nat. Hist. 91(11):8-14.

Whittaker, R.H. 1953. A consideration of climax theory: the climax as a population and pattern. Ecol. Monogr. 23:41-78.

14.

RESTORATION OF NATIVE ECOSYSTEMS

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ABSTRACT

There is little published information on "near-natural" ecosystems and their restoration. Ecosystem restoration involves the setting of a date to indicate a restoration point (e.g., 1778 for the National Park Service in Hawai'i) and presupposes some knowledge of ecosystem status at the target date and time. In Hawai'i, knowledge of past conditions is usually precluded by the rapidity and magnitude of recent changes. However, some restoration efforts based largely on removal of alien organisms have resulted in recovery of ecosystems that are largely native but lack components and processes destroyed in the past by alien organisms including man. No cost estimates for ecosystem restoration in Hawai'i are available as yet. Efforts devoted to prevention of the degradation of prime examples of near-natural and natural Hawaiian ecosystems should at least be equal to restoration efforts.

INTRODUCTION

The concept of "restoration" of an ecosystem implies that certain relatively recent changes are being reversed or that the ecosystem is reverting to what it was at some former time. Ecosystems may range from completely natural ones to those wholly induced by human activities, but the term "restoration" connotes that the recent changes which led to the present condition were in some way undesirable, and that the changes which will now be made will restore some state more desirable than the present, at least in the view of some human stewards.

This paper describes some of the concepts involved in ecosystem restoration, indicates the difficulties involved in undertaking such projects, and reviews some of the efforts at native ecosystem restoration in Hawai'i.

VARIOUS CONCEPTS OF ECOSYSTEM RESTORATION

In nature a number of landscapes (and ecosystems) exist. Duffey (1970) suggested categorizing these as:

1. natural landscapes, unmodified by human activity,
2. near-natural landscapes, with primarily native plants and animals, in areas used by humans, but so far as known, never subject to any major change in land use,
3. semi-natural landscapes, such as pastures and heathland, which have developed as a consequence of human cultural activity and land-use, and
4. artificial landscapes, such as strip-mined areas and areas reclaimed from the sea (e.g. polders in the Netherlands), which are wholly anthropogenic.

Nearly all of the literature on the restoration of ecosystems deals with methods that can be employed to grow something (almost anything) on artificial landscapes. Some good examples of recent work on strip-mined areas were reported by Goodman (1974), Cook (1976), and Hutnik and Davis (1976). Hutchinson (1974) also discussed the natural restoration of ecosystems on ancient spoil-heaps and mine tailings in Great Britain.

Less has been published on the restoration of semi-natural landscapes. Papers on this subject have tended to emphasize the need to use such tools as grazing and burning to maintain these ecosystems at a successional disclimax (Harrison 1974; Kumari 1974; Miller and Watson 1974; and Putwain, Gillham and Halliday 1982).

Although an important objective of many conservation activities is the restoration of near-natural landscapes, much less information has been published on this subject. Two reports of this type deal with the restoration of seagrass communities (Thorhaug and Austin 1976) and tropical high-forests (Kio 1981). Thus the papers presented at this symposium will contribute much-needed information.

PROBLEMS IN ADEQUATELY CHARACTERIZING ECOSYSTEMS

If one is to undertake the restoration of an ecosystem, it is important to know as much as possible about both the present state of the ecosystem and its past history. Yet such information is rarely available for any ecosystem. The reasons for this lack of information are:

1. Few natural ecosystems of any reasonably large size have been adequately described. While species lists for vascular plants and vertebrate animals are usually available, and biomass data for these groups of

organisms are sometimes available, almost no data are usually reported on lower plants, invertebrate animals, fungi, terrestrial algae, or prokaryotes. Even when such information is compiled at present, little or no information on past conditions is available.

2. Natural ecosystems, even those usually described as "stable," are really dynamic and constantly changing. Among the reasons for this are:

(a) the individual species in the ecosystem are continually evolving,

(b) loss of species from, and recruitment of species to, the ecosystem are continually occurring,

(c) successional changes may be occurring,

(d) there may be long-term changes in both climatic and edaphic factors in the ecosystem.

Even with these limitations, it still seems to be generally desirable to attempt to accomplish projects in ecosystem restoration. However, project planners should recognize the difficulties involved in such an undertaking, and recognize that as a practical matter the detectable restoration is likely to be limited to changing the proportions of certain higher plants and vertebrate animals in the ecosystem.

GOALS AND OBJECTIVES OF ECOSYSTEM RESTORATION

As we discuss the restoration of native ecosystems at this symposium, the objectives seem really to be the conservation of natural and near-natural ecosystems; the protection of rare, threatened, or endangered species in these ecosystems; and in some cases the restoration of semi-natural ecosystems to the near-natural state. These are basically the objectives of most conservation activities in national parks and natural areas, and it seems useful to consider what previous workers have stated as appropriate goals for such activities. Elton (1958) indicated that one of the chief aims of conservation should be the retention or replacement in the landscape of the greatest ecological variety, while Berry (1974) urged retention of the greatest genetic variety. One or both of these goals have been given by most subsequent authors, including Duffey and Watt (1971), O'Connor (1974), Polunin and Eidsvik (1979), and Foster (1980). Stankey (1982) described the need for developing management systems to aid in reaching these goals.

When planning for ecosystem restoration it is necessary to choose some date in the past to indicate the point to which the ecosystem should be restored. For the U.S. National Park Service this date was chosen by the Leopold Committee in 1963: "As a preliminary goal, we would recommend that the biotic associations within each park be maintained, or where necessary recreated, as nearly as possible in the condition that prevailed when the area was first visited by the white man" (Barbee 1976). Barbee went on to describe the philosophical problems facing the park manager in Hawai'i if one must manage resources to include Polynesian introduction but exclude those which are post-Cook. At least this policy provides the clearly stated goal that ecosystem restoration projects in Hawaiian national parks should aim at restoration to the state prevailing in January, 1778 (if only we knew what that was).

EFFORTS AT ECOSYSTEM RESTORATION IN HAWAI'I

Most efforts at ecosystem restoration in Hawai'i have involved the use of exclosures; these have been discussed thoroughly in the paper by Loope and Scowcroft (this volume). However, a few more projects have extended beyond the boundaries of exclosures, and these warrant mention.

One such project was the restoration of Laysan Island, in the northwestern Hawaiian Islands. In the early years of this century the vegetation of Laysan was devastated by rabbits. Most of the native flora disappeared (and 3 of the 5 endemic land birds became extinct). Efforts to replant the Island were made in the 1920's with a wide range of plant materials both native and alien (Christophersen and Caum 1931; G.P. Wilder, n.d.). Studies made in the 1960's (Lamoureux 1963) revealed that the ecosystem had been restored to the extent that most of the plants which had previously occurred there were again there, and most of the planted species, both those native to the main Hawaiian Islands and the alien species, had not survived. While there were originally a few local endemics, some of which probably survived the devastation as buried seeds, many reestablished species were fairly widely distributed coastal plants that may well have colonized naturally since 1923. The endemic avifauna fared much worse than the higher plants. Nothing was known of the insects before the devastation, so no comparisons were possible. There is little evidence to suggest that human activities contributed in any substantial way to the restoration of the Laysan ecosystem in the 35 years after the rabbits were removed.

Other projects involved areas in the main islands of the Hawaiian group. In the mid-1930's, after studying the vegetation of the southeastern corner of O'ahu, Egler (1939) proposed that, in the absence of continued disturbance, native Hawaiian plants would eventually replace the alien plants which at that time dominated the area. This hypothesis has never been tested since many of Egler's study sites have been replaced by houses. However, Hatheway (1952) arrived at similar conclusions based on his research in Mokule'ia, northwestern O'ahu. Twenty years after Hatheway established his plots, they were relocated and restudied by Wirawan (1972). He found that in some plots the proportions of native and alien plants had remained essentially unchanged, while in some other plots the proportion of aliens had increased. He concluded that the 20-year interval was perhaps not long enough to permit adequate testing of the hypothesis. The question remains unanswered.

The removal of goats from Hawai'i Volcanoes National Park was enhanced by the appearance of conspicuous undescribed endemic Canavalia in an exclosure, as described by Loope and Scowcroft (this volume), and subsequent studies have been made (Mueller-Dombois, 1979, 1981; Mueller-Dombois and Spatz 1975) of the vegetation changes in the lowland areas of the Park after relaxation of goat foraging pressure. This is a situation opposite to that described earlier, in which grazing was used to restore certain European ecosystems to the stage desired for conservation (Kumari 1974) by preventing the normal sequences of succession from occurring. In the Hawai'i Volcanoes case, succession has proceeded rapidly following goat removal. At the present time certain alien plants are dominant in the succession in much of the area, but the climax stages are as yet not evident.

While one study suggested that pig digging in grasslands on Mauna Loa greatly increased the percentage of alien species in communities which had formerly had more native species (Spatz and Mueller-Dombois 1975), other studies in rain forest areas have yielded inconclusive results to date (Loope and Scowcroft, this volume); however, there is evidence in at least some plots of recovery of native species.

It had long been suspected that sheep and other feral herbivores were responsible for a decline in mamane (Sophora chrysophylla) forests; so it had been predicted that the removal of these herbivores would result in restoration of this forest ecosystem. However, there was little scientific evidence for this. Recently, papers (Scowcroft 1983; Scowcroft and Giffin 1983; Scowcroft and Sakai 1983) have provided data which support these hypotheses and demonstrate that ecosystem recovery and an increase in cover by native species occur once the herbivores have been removed in this forest type.

The most conspicuous effort in Hawai'i in reintroducing a native species to the wild in order to restore a conspicuous component of an ecosystem is the nene (Nesochen sandvicensis) restoration project. It has been demonstrated that nene can be bred in large numbers in captivity and released into the wild where they can feed and reproduce. However, there is a high mortality rate in the wild, and the wild population at present can be maintained only by continual reintroductions of captive-reared birds. Research is under way to determine what is happening to birds after release. The most recently published study (Stone, Hoshide, and Banko 1983) did not confirm the hypothesis that predators such as mongooses, feral cats, feral dogs, or pigs play a critical role in reducing wild populations of nene, but the study included only a small number of birds in only one part of the species range. In sum, the factors limiting restoration of the nene are still unknown but probably are complex (Stone et.al. 1983).

COSTS OF ECOSYSTEM RESTORATION

It is difficult to determine costs and benefits of ecosystem restoration. Thorhaug and Austin (1976) gave costs of planting seagrasses from seed in areas where the original cover had been destroyed. Their cost estimates ranged from about $21,000 to $140,000 per hectare depending on density of planting, and they concluded that restoration was feasible at those costs.

Gosselink, Odum, and Pope (1974) worked in the opposite direction and attempted to determine the economic value of the tidal marsh. They concluded that when all uses of the marsh are considered, including direct production of fish and shellfish, its value in assimilating waste, and its gross primary productivity, its total social value was in the range of $50,000 to $80,000 per hectare.

I am unaware of any comparable figures that have been developed for Hawaiian ecosystems, or of any cost/benefit studies that have been undertaken on the value of native ecosystems. While it would be possible to estimate costs to date for removal and exclusion of goats from Hawai'i Volcanoes National Park, or for the nene restoration project, neither project is yet completed, and it is premature to attempt to develop even relatively simplistic cost/benefit ratios.

CONCLUSIONS

While few ecosystem restoration projects have yet proceeded far enough in Hawai'i to enable workers to predict their probable outcomes, results to date suggest that the following sorts of manipulative techniques will need to be used in conducting them:

1. Removal of non-native herbivores and prevention of their re-introduction.

2. Removal of non-native predators and prevention of their re-introduction.

3. Removal or drastic control of alien plants, at least those determined by study to form significant components of the ecosystem.

4. Replanting with rare native plants which are as genetically similar as possible to those which formerly inhabited the area.

5. Restocking with rare native animals which are as genetically similar as possible to those which formerly inhabited the area.

6. Preventing, or at least slowing, detrimental changes in the ecosystems before, during, and after restoration. (This may well be the most difficult task of all.)

Even when all these techniques are fully employed it will probably not be possible to reach a goal such as that of restoring ecosystems in national parks to late eighteenth century stages, simply because we don't know what these were; it is likely that many species then present have become extinct already anyway. This does not mean that such efforts should not be undertaken, but does suggest that equal efforts should be devoted to prevention of further degradation of Hawaiian ecosystems.

LITERATURE CITED

Barbee, R.D. 1976. Ecological park management: a manager's perspective. Proc. 1st Hawaii Volcanoes Natl. Park Nat. Sci. Conf., 35-38. Honolulu: Univ. Hawaii.

Berry, R.J. 1974. Conserving genetical variety. In Conservation in practice, ed. A. Waron and F.B. Goldsmith, 99-115. London: John Wiley Sons.

Christophersen, E., and E.L. Caum. 1931. Vascular plants of the Leeward Islands, Hawaii. B.P. Bishop Mus. Bull. 81.

Cook, C.W. 1976. Surface-mine rehabilitation in the American West. Environ. Conserv. 3(3):179-183.

Duffey, E. 1970. Conservation of nature. London: Collins.

Duffey, E., and A.S. Watt, eds. 1971. The scientific management of animal and plant communities for conservation. Oxford, England: Blackwell Sci. Pub.

Egler, F.E. 1939. Indigene vs. alien in the development of arid Hawaiian vegetation. Ecology 23(1):14-23.

Elton, C.S. 1958. The ecology of invasions by animals and plants. Oxford, England: Methuen.

Foster, R.B. 1980. Heterogeneity and disturbance in tropical vegetation. In Conservation biology, ed. M.E. Soule and B.A. Wilcox, 75-92. Sunderland, Mass.: Sinauer Assoc., Inc.

Goodman, G.T. 1974. Ecological aspects of the reclamation of derelict land. In Conservation in practice, ed. A. Waron and F.B. Goldsmith, 251-264. London: John Wiley Sons.

Gosselink, J.G., E.P. Odum, and R.M. Pope. 1974. The value of the tidal marsh. Cent. for Wetland Resour. Pub. No. LSU-SG-74-03. Baton Rouge, La.: Louisiana State University.

Harrison, C.M. 1974. The ecology and conservation of British lowland heaths. In Conservation in practice, ed. A. Waron and F.B. Goldsmith, 117-129. London: John Wiley Sons.

Hatheway, W.H. 1952. Composition of certain native dry forests: Mokuleia, Oahu, T.H. Ecol. Monogr. 22(2):153-168.

Hutchinson, J. 1974. Land restoration in Britain--by nature and by man. Environ. Conserv. 1(1):37-41.

Hutnik, R.J., and G. Davis, eds. 1976. Ecology and reclamation of devastated land. Vol. 1. New York: Gordon and Breach.

Kio, P.R.O. 1981. Regeneration methods for tropical high-forests. Environ. Conserv. 8(2):139-147.

Kumari, E. 1974. Man-made ecosystems and nature conservation, with special reference to Matsulu Bay, Estonian SSR. Environ. Conserv. 1(1):31-36.

Lamoureux, C.H. 1963. The flora and vegetation of Laysan Island. Atoll Res. Bull. 97.

Loope, L.L., and P.G. Scowcroft. Vegetation response within exclosures in Hawaii: a review. [This volume]

Miller, G.R., and A. Watson. 1974. Heather moorland: a man-made ecosystem. In Conservation in practice, ed. A. Waron and F.B. Goldsmith, 145-166. London: John Wiley Sons.

Mueller-Dombois, D. 1979. Succession following goat removal in Hawaii Volcanoes National Park. Proc. 1st Sci. Res. Natl. Parks Conf., 1149-1154. San Francisco: Natl. Park Service.

Mueller-Dombois, D. 1981. Vegetation dynamics in a coastal grassland of Hawaii. Vegetatio 46:131-140.

Mueller-Dombois, D., and G. Spatz. 1975. The influence of feral goats on the lowland vegetation in Hawaii Volcanoes National Park. Phytocoenologia 3(1): 1-29.

O'Connor, F.B. 1974. The ecological basis for conservation. In Conservation in practice, ed. A. Waron and F.B. Goldsmith, 87-98. London: John Wiley Sons.

Polunin, N., and H.E. Eidsvik. 1979. Ecological principles for the establishment and management of national parks and equivalent reserves. Environ. Conserv. 6(1):21-26.

Putwain, P.D., D.A. Gillham, and R.J. Holliday. 1982. Restoration of heather moorland and lowland heathland, with special reference to pipelines. Environ. Conserv. 9(3):225-235.

Scowcroft, P.G. 1983. Tree cover changes in mamane (Sophora chrysophylla) forests grazed by sheep and cattle. Pac. Sci. 37(2):109-119.

Scowcroft, P.G., and J.G. Giffin. 1983. Feral herbivores suppress mamane and other browse species on Mauna Kea, Hawaii. J. Range Manage. 36(5):638-645.

Scowcroft, P.G., and H.F. Sakai. 1983. Impact of feral herbivores on mamane forests of Mauna Kea, Hawaii: bark stripping and diameter class structure. J. Range Manage. 36(4):495-498.

Spatz, G., and D. Mueller-Dombois. 1975. Succession patterns after pig digging in grassland communities on Mauna Loa, Hawaii. Phytocoenologia 3(2/3): 346-373.

Stankey, G.H. 1982. The role of management in wilderness and natural-area preservation. Environ. Conserv. 9(2):149-155.

Stone, C.P., H.M. Hoshide, and P.C. Banko. 1983. Productivity, mortality, and movements of nene in the Kau Desert, Hawaii Volcanoes National Park, 1981-1982. Pac. Sci. 38(3):301-311.

Stone, C.P., R.L. Walker, J.M. Scott, and P.C. Banko. 1983. Hawaiian goose research and management--where do we go from here? Elepaio 44(2):11-15.

Thorhaug, A., and C.B. Austin. 1976. Restoration of seagrasses, with economic analysis. Environ. Conserv. 3(4):259-267.

Wilder, G.P. n.d. Notebooks and letters. Dep. Botany, Univ. Hawaii, Honolulu.

Wirawan, N. 1972. Floristic and structural development of native dry forest stands at Mokuleia, N.W. Oahu. M.S. Thesis, Univ. Hawaii, Honolulu.

15.

GENETICS, MINIMUM POPULATION SIZE, AND THE ISLAND PRESERVE

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ABSTRACT

Small populations are often extinction-prone because they are too small demographically or because they contain too little genetic diversity to adapt to change or to give rise to new species. In the genetic context, minimum effective population size may be defined as that level in which 90% of genetic diversity is retained over evolutionary time. Genetic diversity may be maintained within populations or among populations of a species. In outbreeding species, extinction can be precipitated by loss or skewing of allele frequency through genetic drift and by loss of alleles through small population sampling effects. Inbreeding depression (including increasing genetic load) results in lowered survival and ultimately population decrease. In typically inbreeding and polyploid species, where genetic variability is stored among populations, loss of populations is an important step in the process of extinction. Lack of genetic variation within populations reduces ability to adapt to the catastrophic changes often brought about by man, and also predisposes populations of these species to extinction. Hawaiian endemics resulted from colonization by small groups or single founders and many of these may have been subjected to repeated bottlenecks adapting them to small population size and inbreeding. Management approaches to alter survival probabilities include increasing gene flow among captive individuals and populations to enhance genetic diversity, and mate manipulation to adapt small captive populations to inbreeding and minimize inbreeding depression. When management increases adaptation to inbreeding, efforts to also increase population size rapidly will decrease the probability of inbreeding depression and help reduce loss of rare alleles remaining in a population. Hawaiian species that are present in moderate numbers but are threatened or that appear to have recovery potential from smaller population size should be subjected to the

following analysis: 1) determine population isolation and adaptation to inbreeding; 2) if population is so adapted, separate and isolate small founder populations throughout habitat pockets; 3) if populations are not adapted to inbreeding, establish several small captive populations for inbreeding and eventual reintroduction; and 4) consider use of controlled backcrossing to regenerate variability and plan for eventual reintroduction.

INTRODUCTION

During the last few thousand years, the Hawaiian Islands have experienced rapid and large scale extinctions. Recently, lands have been set aside in preserves and parks to protect habitats and populations of endemic species, yet population declines continue. The number of species able to survive will be determined, at least indirectly, by the shape of parks and reserves, their numbers, sizes, and surrounding land uses, and the distances between reserves. Even if ecosystem deterioration ceases, the total capacity of the Islands for native species will obviously be far less than was historically possible before colonization by humans.

Habitat loss and continued presence of alien species populations greatly accentuate the protected habitat and island isolation effects that characterize Hawaiian endemics. Thus, declines continue regardless of the effectiveness with which boundaries of parks and preserves are protected. Trends to extinction can be countered through habitat accession and restoration, innovative defenses of preserve boundaries, and innovative management of declining populations. While the odds are strongly against success, there are new and promising developments in habitat and population restoration techniques that are worth pursuing.

In addition to its habitat, each species has basic requirements for reproduction and evolutionary survival that are strongly influenced by population numbers, sizes, and gene exchange. While some characteristics predispose some species to difficult times in rapidly changing environments, others predispose more flexible species to colonize under changing environmental conditions. When populations are small and isolated, their basic predispositions for colonizing or for extinction are accentuated.

Genetic characteristics of species determine how they will respond to preserve design and management. Design and management will determine what levels of isolation and dispersion of genetic diversity will exist within the protected area for any given species

(Soule and Wilcox 1980). Inevitably, when species distributions and movements are restricted to isolated protected areas, natural patterns of gene exchange and rates of evolution are affected. Restrictions on distribution and movement are often imposed by factors not related to natural events. For example, preserve boundaries rarely coincide with natural species distributions but are largely politically determined (Schonewald-Cox and Bayless, in prep.). It is therefore not surprising that boundaries, invasions and adjacent land uses are likely to present novel selection pressures (Liu and Godt 1983), with which genotypes of endemic species are frequently unequipped to cope.

The increasing modifications of natural gene exchange have powerful applications for conservation: for planning the preventive medicine of conservation, for diagnosing predispositions toward population decline, for detecting pending extinctions, and for administering measures intended to restore populations to "evolutionary" health (Schonewald-Cox et al. 1983). This paper focuses on the small population and explores practical techniques for maintaining the evolutionary health of populations and reversing declines in Hawaiian endemic populations.

WHY DO POPULATIONS BECOME SMALL?

Populations become small as a result of many environmental and selection variables (Beardmore 1983; Nei 1975). Catastrophic impacts, such as volcanic explosions, prolonged changes in climate, or new biological invasions, have probably accounted for the vast majority of declines and extinctions in past geological time. However, direct habitat elimination and exploitation, predation, disease, parasitism, and competition by newly introduced species have accounted for the loss of at least 60% of Hawaiian endemic bird species alone and undetermined numbers of other animal and plant endemics in the very constricted time period of 5,000 years (Olson and James 1982a and 1982b; James and Olson 1983; Atkinson 1977). Thus, populations can become small for a variety of reasons, and the rapidity with which extinctions are now occurring suggests that they are more cause- than time-dependent.

SMALLNESS AND SURVIVAL

From the standpoint of evolutionary genetics, species with genetically impoverished populations and species which have a narrow range of environmental tolerance are the most susceptible to extinction (Carson 1983; Beardmore 1983; Soule 1983). Smallness of populations is in itself a threat to many species, especially those that require large gene pools and depend upon large amounts of gene flow for survival (Ralls, Brugger, and Ballou 1979; and Wright 1977 give examples for mammals). These species suffer from inbreeding depression and loss of genetic diversity when their populations become small. (Conversely, when gene flow is too rapid or barriers between previously distant populations are broken down, the swamping effect can be equally damaging, resulting in an outbreeding depression or heterosis.)

Species that typically inbreed or self-fertilize are likely to survive if they are flexible. Flexibility is limited by the amount of genetic diversity (alternate alleles and complex inter-gene relationships) carried by the genotype (Liu and Godt 1983; Clegg and Brown 1983). Nei, Maruyama, and Chakraborty (1975) demonstrated that a population must be quite small to lose substantial allelic diversity. Alternatively, if the population lacks diverse genotypes, then species survival requires the availability of other populations for recolonization (Selander 1983).

WHAT IS A SMALL POPULATION?

A population can be considered small with one or a thousand individuals, depending upon characteristics of the species. A "small" population is extinction-prone because it is demographically unstable or possesses too little genetic diversity to retain its evolutionary potential (e.g., ability to adapt and potentially give rise to other species). A population which retains about 90% of its genetic diversity is said to be at or above the genetic estimate of minimum effective population size and is said to retain its long-term evolutionary potential. On the other hand, a small population (below the minimum effective population size) retains too little diversity and is prone to too many genetic problems to maintain its evolutionary potential (e.g. ability to adapt and potentially give rise to other species).

Effective Population Size

The "effective population size," usually referred to as N_e, is the theoretician's parallel to the actual population size and is based in part on the number of males and females contributing to offspring in any one generation. Several baseline assumptions are made in determining the effective population size. In the case of small populations, N_e is the size an ideal population would have to be in order to experience the same rate of drift and decrease in variability as the study population. For example: In a study population of 50 individuals, there may be only 2 males and 10 females that mate to produce 1 offspring per female in the following year. A crude estimate of the effective population size would be about 12. The effective population size is derived and described in varying levels of detail in evolutionary and population biology references. (See Wright 1978 and Crow and Kimura 1970 for derivations and theory; and see Frankel and Soule 1981, Soule and Wilcox 1980, and Schonewald-Cox et al. 1983 for use in the conservation context.)

Minimum Viable Population

The objective in conservation is to maintain populations at--or restore them to--levels matching the minimum requirements for survival. There are no fixed formulae for determining the exact minimum requirements for population size. However, some useful attempts have been made to generate estimates. The first estimate was generated by Franklin (1980) based on his analysis of *Drosophila*. The figure of 500 suggested by Franklin is currently being reexamined in light of new developments in conservation biology, genetics, and demography. Soule (pers. comm.) and a number of geneticists and demographers have collaborated to produce a new interpretation of minimum population requirements. Based on homeothermic vertebrate biology, they suggest that a few hundred animals (effective size) are necessary for minimum demographic survival. This number would just maintain population growth despite consistent mortality rates (due to individual cause of death or across-population causes of death). If periodic catastrophic events are included, the "few" hundred required in a stable environment may already be a small number relative to the need for survival.

THE EVOLUTIONARY POTENTIAL OF SMALL POPULATIONS

How genetic diversity is distributed within a population depends upon the mating system and upon environmental selection. Genetic diversity is manifested in several ways. Between populations it is manifested in different allele frequencies, different alleles, and different multi-gene relationships (including polygenes and overdominant genes). Within populations it is manifested in polymorphism, heterozygosity, polygenes, overdominant genes, and polyploidy.

In nature, several opportunities exist for increasing genetic diversity in populations. Beardmore (1983) summarized 4 basic sources of population diversity:

1. Recurrent mutational changes.
2. Inflow of genes from other populations, or species "migration".
3. Stochastic processes such as genetic drift.
4. Some form of selection that favors population diversity.

When populations become small and are isolated, the potential for new genetic variation to enter the gene pool becomes reduced; in addition, genetic diversity within the population is eroded. A small population of a cross-fertilizing species represents only a fraction of the diversity of its original population (sampling effect).

Typically Out-Breeding Diploid Species

For typically out-breeding species, 2 principal interacting factors can precipitate extinction. First, there is genetic drift which occurs even before the population becomes small. Genetic drift is the random loss of alleles and change in allele frequencies that result from sampling with each sexual reproduction. Alleles that occur in non-reproducing individuals decrease in frequency in the population, and if they are rare alleles and occur exclusively in individuals which have not reproduced, they are then lost altogether from the population unless they are restored by immigrants from another population (gene flow).

Secondly, there is the sampling effect of the population reduction itself. In a small population, more is lost than rare alleles. The otherwise normal genetic drift is exaggerated synergistically by the loss of some rare and potentially common alleles because fewer individuals remain to reproduce. These remaining individuals represent only a fraction of the allelic diversity of the original population. Thus, there is not only a change in allele frequencies, but an outright loss of alleles as well. Futuyma (1983) suggested that this extreme sampling generally results in a decrease in frequency of beneficial alleles and a concurrent increase for deleterious ones.

As population size decreases, allele diversity declines more and more due to the sampling effects of genetic drift and population reduction mentioned above. This is manifested in narrower mate selection which increases the likelihood of mating between individuals related by descent. Inbreeding, when it occurs in a species that is not adapted to this sort of mating strategy, can overtake the initial cause of population declines and drive populations to extinction. When related individuals mate, deleterious recessive alleles that are normally hidden in heterozygous recessive condition are expressed homozygously. The array of deleterious, recessive alleles is called genetic load. Genetic load occurs in the genome at a rate that is relatively constant for each species. It is speculated that 1-1.5% of alleles in humans are deleterious, but genetic loads for most species are unknown. Inbreeding also disrupts the balance of polygenes (Carson 1983), and it can interfere with or eliminate overdominant genes (Futuyma 1983).

When outbreeding species are forced into inbreeding, "inbreeding depression" results from the interaction of the following: the expression of deleterious recessive alleles caused by inbreeding; the loss of alleles caused by the sampling effect of small population size; and the increasingly reduced representation of alternate alleles in the population. The combined effects of these are lower survival rates and eventual population decline.

To summarize, the most serious consequences of small population size for species that store genetic diversity within the population are loss of alleles and inbreeding depression and population decline.

Polyploid and Typically Inbreeding and Self-Fertilizing Species

In polyploid species, which are typically inbreeding and self-fertilizing, inbreeding and loss of allelic diversity within the population do not pose the same threats to survival as they do to diploid, outbreeding species. However, even in its ultimate form of self-fertilization, inbreeding leads to a uniformity in the population which makes the population especially vulnerable to climatic or other environmental changes. Loss of variability may not become serious in the absence of habitat change or when selection is relaxed. However, environmental, social or ecological stresses may require characteristics that genetically depauperate populations have lost. One of the most serious consequences of small population size for species that store genetic diversity between populations is the loss of genetic sources (other populations for recolonization), should local extinction occur.

DIFFERENCE BETWEEN SMALL POPULATIONS NOW AND AT INITIAL COLONIZATION

Species that first colonized the Islands experienced stresses likely related to levels of inbreeding, as well as changed food or climate regime and geological stresses; but competition stress was probably not a factor. Progressive colonization by diverse species together with their expansions and divergences eventually led to competition stress.

Disequilibrium -- Adaptation

Environmental stresses peculiar to the Hawaiian Island chain probably changed over tens or hundreds of thousands of years. Species had to continuously adapt to these changes in order to survive into the paleoarchaeological period. This period changed the rate of mortality of individuals and consequently of species. Selection pressures for adaptation to direct and indirect human modification of habitat intensified, only to reach cataclysmic proportions in the last few hundred years. Mutation rates are not known to accelerate in response to habitat deterioration, intense predation, depredation or competition. Changes by either mutation or recombination occur in response to generation time and population growth rates.

Threatened and endangered endemics have experienced negative population growth rates. Therefore the opportunity for adaptation has, if anything, decreased while the demand for adaptation has accelerated. For example, the extreme changes of stream temperatures to as much as 10 to 11 C above normal (in daily fluctuaion as well as the absolute temperature, J.D. Parrish, pers. comm.) exclude native Hawaiian freshwater fishes and favor alien species competitors. The latter, being tolerant of temperature fluctuations, are now replacing endemics in reconstructed cement-lined stream channels, adding competition to the temperature stress of endemics.

Disequilibrium -- Species Turnover

Selection processes (now influenced by man) do not recognize value differences between endemic and alien species that man does. By attributing value to some species that can no longer survive on their own and eliminating others that would normally replace the declining ones, man decreases the ease with which some ecosystems can sustain themselves, and increases the difficulty we will face in trying to maintain evolutionary dynamics of native species in the Islands. Selection pressures have changed in category and intensity over the past several hundred years as a result of natural events and man's influences. Selection is now demanding adaptational changes on the part of endemics which they may never have had the capability of meeting, since their previous successes were based on entirely different packages of tolerances and pressures.

ASSESSING AND IMPROVING A SMALL POPULATION'S CONDITION

Fortunately for the conservation community, the agricultural and sporting industries have had an age-old interest in manipulating small populations (cattle, Bos taurus; goats, Capra hircus; horses, Equus caballus; pigs, Sus scrofa; cats, Felis catus; dogs, Canis domesticus; decorative plants, etc.). While the techniques they employed were not, and frequently still are not, developed from population or evolutionary genetic theory, the practical experience and techniques derived from trial and error have contributed a great deal of guidance on the preventive and remedial measures useful for dealing with captive populations. The cattle industry, for example, has used the practice of maintaining stud books and pedigrees which recently has been combined with newly acquired knowledge of genetics to develop inbred lines of cattle that are now free of any lethal characteristics (Lasley 1978). Borrowing from this technology, some of the major zoological parks have begun to record pedigrees in order to determine levels of inbreeding (see Ballou 1983) and thereby influence reproductive success (Foose 1983; Ralls, Brugger, and Ballou 1979; Ralls and Ballou 1983).

There is a 180-degree difference in the evolutionary implications of management objectives of the cattle breeder and those of the manager of species for conservation. Typically, commercial interests impose heavy selection and controlled mating in order to narrow the characteristics expressed by a line to a specific set of desired qualities. Those qualities must occur with predictable intensity every time members of the line are mated. Inbred lines that are free of lethal alleles are especially prized. The breeder also hopes that the line will exist in "perpetuity" (in commercial terms, the lifetime of the breeder's economic motive or company). Because the environment in which the animal or plant lives can be controlled almost entirely, the breeder may feel that there is no need to maintain within-individual variability--at least it does not seem so for the evolutionary short term--but lack of genetic alternatives make the industry particularly vulnerable. If, with wheat for example, a new disease appears to which none of the domesticated strains have any resistance, the distance between mass human starvation and sufficient wheat may be measured by the availability of alternate and variable genotypes.

Populations ex situ

The optimum objective of zoological park conservation programs is to maintain populations for eventual restoration to the wild. Zoological park breeding programs follow 2 management approaches to accomplish this objective.

The first approach consists of obtaining animals from the wild which are then bred and periodically exchanged with other institutions. This provides gene flow between captive populations. These captive or semi-captive populations serve to stock other zoological parks and furnish the eventual founders for restoration programs. Frequently, though not always, numerous sources exist for gene flow so that considerable genetic diversity is stored in the whole of the international captive network (see Flesness, Grahm, and

Hastings 1982; and for International Species Inventory program (ISIS), see Foose 1983; Benirschke 1983).

In the second management approach, inbreeding is used deliberately when only a very few individuals exist in captivity and none are available from the wild to provide gene flow. In this case, inbreeding is totally unavoidable if the species is to continue. This approach is also used when a population is to be kept small and isolated, e.g. for exhibits, with no intention to restore members to native habitats. In this approach, mate selection is manipulated to adapt the population to inbreeding while simultaneously minimizing inbreeding depression.

In both management approaches, unlike those in commerce, the objective is to minimize selection (with the exception of selection for inbreeding tolerance in the second approach) and to avoid loss or skewing of allele frequencies. This is a very difficult task. Inadvertent selection introduced by diet, pen conditions, and veterinary care may increase selection pressures not favorable to eventual restoration of the species to the wild. Alternatively, management may unintentionally reduce selection for alleles of special value to survival in the wild. The strategy that managers of zoo populations take to minimize unnecessary impositions of selection is to spread mating among the largest number of individuals or to increase gene flow when possible by including individuals from wild populations.

Under captive conditions, it is possible to record which animals are being mated and to maintain a pedigree that is checked every time a choice of mates is to be made. This reduces accidental matings between individuals related by descent and significantly improves survival for captive populations. Ballou (1983) demonstrated in detail how the pedigree can be used to calculate the inbreeding coefficient. The inbreeding coefficient is a valuable tool for determining whether, and to what extent, individuals are inbred.

<u>Populations in situ</u>

Unfortunately, in conditions such as those that exist surrounding semi-wild or free-roaming populations, mating cannot usually be controlled nor can pedigrees be easily maintained, even if mating behavior is monitored. For example, with some carnivores, ungulates or primates, and many other groups, attempted fertilizations can involve more than one male, and it cannot be determined exclusively from field observations which male is actually responsible for fertilization. Hence, it is difficult to establish population health genetically.

Laboratory techniques, such as isozyme electrophoresis and karyotyping, can estimate the amount of variability in populations (Benirschke, Lasley, and Ryder 1980; Allendorf 1983; Hamrick 1983; Chambers and Bayless 1983) or can detect abnormal chromosome numbers or gross mutations in the chromosomes. However, these techniques provide no useful information for estimating levels of inbreeding in non-captive populations. A search for alternate means of determining inbreeding coefficients when no pedigree is available has revealed that mitochondrial DNA (mtDNA) analysis may have the greatest promise. (See Powell 1983 for a discussion and example of mtDNA analysis for the mosquito *Aedes aegypti*.)

Because of its potential benefit to conservation of species in natural habitats, the method and use of mtDNA analysis deserves some description. Fortunately, the technique has gone beyond use with *Drosophila* and is presently being applied to vertebrate populations, e.g. lizards (A.R. Templeton, pers. comm.). Analysis of mtDNA involves the electrophoresis for DNA segments that are cut by restriction endonucleases at specific recognition sites. The DNA of the mitochondrion is single stranded and circular (reminiscent of bacterial DNA) and can be mapped, cut and accounted for far more easily than the vastly larger and more complex system of nuclear chromosomes. Because mitochondria are generally inherited with the egg, they can act as tracers for female lineages with a small margin of error. The experiments presently being conducted use pedigree data and anatomical markers to test the reliability of the assumptions of heritability and uniqueness of markers for each individual. The mtDNA technique has the potential of circumventing the use of pedigrees for detecting inbreeding levels. Depending upon species chromosomal arrangements and sexual dimorphism of chromososmes and gametes, additional markers can be applied to males (as on the Y chromosome).

So far, researchers are using both female (mtDNA) and male (sexual or autosomal) markers. It may not be easy to identify male markers for many species stressed in conservation programs, and until male markers are identified, it is desirable that we find an interim method, even if it is less exact. One such method would combine the results of mitochondrial analysis with known data on relevant population and behavioral parameters for inference of an approximated inbreeding coefficient. This approximated coefficient then could be used similarly to properly document inbreeding coefficients for planning population management. It is hoped that, based on controlled laboratory experiments, a predictable margin of error for the inference could be established.

CONDITION OF HAWAIIAN ENDEMICS

The entire native fauna and flora in the Hawaiian Islands was established from small groups of founders or single colonizers that, for the most part, never received subsequent gene flow from any mainland or other island.

Surviving Colonization

In order for a species to survive colonization with only one or a few founders, it must be able to withstand the deleterious effects of inbreeding and the other stresses of small populations (Carson 1983). This can occur in several ways, including combinations of the following, if:

1. The founder is self-fertilizing.
2. The founder is an immigrant from an already inbred population.
3. The founder carries few deleterious alleles, or the deleterious alleles carried are not lethal in the new environment even though they may have decreased overall fitness.
4. The founder successfully reproduces, competes for, and expands its range in the habitat, and competes successfully to maintain the niche.
5. The founder experiences selective release with abundant food source and no (or little) predation.
6. The founder finds an abundance of resources and open niche space.
7. One or more additional founding events by the same species occur soon after the initial one, though it may not necessarily be from the same source.

Historical Influences on Survival

It may be that during their initial colonization period, Hawaiian endemics experienced a strong, internally directed selection to overcome small population size and inbreeding depression. As the numbers of species increased on the Islands, such factors as predation and competition, combined with environmental fluctuations, may have kept populations small or subjected them to repeated bottlenecks. Many Hawaiian endemics may have been already adapted to inbreeding and small population size early in their island histories. Regardless, with the arrival of humans on the Islands, reduction in population sizes caused by hunting, coupled with severe environmental selection caused by invasions of alien organisms, habitat elimination, and relegation of populations to marginal habitats, necessarily intensified selection for tolerance of small population size and inbreeding tolerance.

The work of Olson and James (1982a, b; James and Olson 1983) suggested that the first major extinctions of Hawaiian endemic bird species began about 1,500 years ago. The agents of destruction were human: deforestation carried out for the benefit of agricultural development, introduction of the rat (Rattus exulans) and pig (accompanists of the Polynesians; Atkinson 1977), and hunting of flightless species for food. In 1982, the published results of Olson and James (1982a, 1982b) pointed to the extinction of approximately one-half of the Hawaiian endemic bird species while Polynesians occupied the Islands; only about one-third of the original diversity remains after the appearance and settlement by contemporary cultures in the Hawaiian Islands. Most radical in their declines were the non-passerine species, including geese, owls, and crows, of which only 15% or fewer remain.

Modern Prospects for Survival

Species plummeting to small population sizes and faced with inbreeding and allele loss are re-experiencing colonization, this time on habitat islands within the Hawaiian Islands. As probably occurred historically with the new arrivals, some species will adjust and survive and some will fail. It will not be possible for all the threatened species to retain and recolonize the identical niches they once occupied. Both species populations and niches have changed permanently in many cases.

Species that are island endemics have no possibilities for range expansion or for the reception of gene flow from sources other than in the Islands. With much of the natural lowland habitat converted to private use, it is reasonable to expect that restorations to levels above minimum effective population sizes for many endemic species near extinction are no longer possible; nor can we foresee that some populations will ever grow beyond the small, and possibly inbred, level in the near future.

This island scenario has its closest parallel (though it is a weak one) in zoo populations of species which are functionally extinct in the wild, and whose populations in captivity are the only hope of preserving the species.

INBREEDING AND HAWAIIAN ENDEMIC DIPLOID SPECIES

In small populations, inbreeding is affected by the sex ratio, mating system, mating system flexibility (or options of several mating systems available to a species), overlap of generations, the number of times the individuals mate, the production of single or many young, and the generation time. Allele loss is aggravated by slow population growth. Inbreeding is aggravated if the sex ratio is unequal (as with polygynous species), and becomes a function of the number of females and males, independently:

$$\frac{1}{N_e} = \frac{1}{4N_m} + \frac{1}{4N_f} \text{ or } N_e = \frac{4N_mN_f}{N_m + N_f}$$

(where N_e is the effective population size, N_m is the number of males and N_f is the number of females) (Frankel and Soule 1981). However, it seems that by far the majority of endangered endemic bird species in the Hawaiian Islands is predisposed to monogamy (Shallenberger 1981), and this type of mating system tends to equalize genetic contributions by individuals. Equalizing contributions to subsequent generations will tend to reduce the rate at which heterozygosity is lost and at which the genetic load is exposed. For species that are not potentially inbred or that still exist in large numbers, monitoring for sudden declines and inbreeding is most essential.

In a study of a polygynous species, North American elk (Cervus elaphus), Schonewald-Cox, Baker, and Bayless (in prep.) conducted an analysis of founding events that were part of restoration programs. They found that conventional restorations tended to use from 4 to 25 individuals with little regard for demographic composition. They hypothesized that the first year's increase in level of inbreeding ranged from 22% to 3.6% (for 4 to 25 individuals respectively) which 20 years later, for example, would cause the populations to have inbreeding coefficients ranging from 1 to 0.41. The safe increase in the inbreeding coefficient given by Lasely (1978) for domestic cattle for one generation is 0.01. For comparison, the inbreeding coefficient of an individual produced by a brother-sister mating in a normal family is 0.25 and for first cousins is 0.06. With time and in the absence of gene flow, the percent relation only increases. While the increases in inbreeding coefficients for monogamous species do not occur as quickly as with polygynous species of the same size, the tendency for inbreeding with small population size for any mating system is still quite high. Species that have gone through bottlenecks have been affected by small population size and inbreeding, and it may very well be that the series of bottlenecks experienced by some declining Hawaiian species may in fact have already converted them to strongly inbred lines. The fact that some of these persist suggests that they may have adapted to inbreeding, at least for the short term.

RESTORING SMALL POPULATION REMNANTS
OF DIPLOID SPECIES WITH INBREEDING: A CASE EXAMPLE

To reverse population decline and inbreeding for Speke's gazelle (Gazella spekei), Templeton and Read (Templeton 1980; Templeton and Read 1983) applied Templeton's findings on the adaptation of Drosophila populations to inbreeding. The Speke's gazelle, numbering 25 when Templeton and Read began the project, originally consisted of 4 founders, 1 male and 3 females. Calculating the effective population size of the founder herd, and incorporating the effects of highly differential contributions by the founders to the progeny, they obtained $N_e = 2$ (where N_e is the effective population size). The population was both inbred and suffering from depression. Taking into account that no other source existed for gene flow and that this species was nearly extinct in the wild, Templeton and Read decided to tackle the problem of inbreeding depression by using a controlled application of inbreeding. The decision to use this approach may be especially pertinent to the current situations existing for endangered Hawaiian species and therefore is described in some detail.

Adapting to One's Genome

First, Templeton and Read (1983) justified adapting a normally outbreeding species to inbreeding by using the hypothesis that individuals in a population are not only adapting to their external environment but to their internal genetic environment as well. Adaptation to genetic load is greatly influenced by the mating system of the species population. Templeton and Read (1983) pointed out that the symptoms of inbreeding depression (changes in fertility, birth weights, survival) are reminescent of the symptoms that result from failure of a species to adjust to rapid environmental changes. Although deaths from inbreeding depression are almost never traceable to a single allele, the death which typically occurs early in life can be said to result from one to several deleterious alleles formerly carried recessively in the genome (see Ralls, Brugger, and Ballou 1979).

Adapting to Inbreeding

Templeton (1980) showed that adaptation to inbreeding can be achieved regardless of population size. That this can be achieved rapidly and successfully is a major breakthrough in the application of genetics to conservation of small populations of non-typically inbreeding species. He suggested that this is done most successfully and rapidly when "genetic variability is maximized" at both the individual and population level. The following summary is a series of "rules" for selecting mates and for achieving the adaptation to inbreeding that is recommended and elaborated upon in Templeton and Read (1983):

First and foremost, the objective is to increase population size as rapidly as possible before and during the implementation of the breeding program.

Secondly, as concerns the selection of characteristics for the mates:

1. Parents, in combination, must maximize genetic variation.
2. Parents must be healthy.

Thirdly, as concerns the selection of characteristics that the offspring will receive from the parents:

1. Offspring should have maximum genetic variability in terms of founder ancestry.
2. Offspring should be the result of inbreeding, but not extreme inbreeding.

In order to accomplish the basic genetic planning for this work, one needs only the pedigree data for the population. Therefore, for any critically endangered population that is maintained in semi-captive or captive conditions, it is essential (to the extent feasible) to maintain pedigree data. (In most cases, where we deal with wild populations, pedigree data are not necessarily available; then the mtDNA techniques discussed in the last section become increasingly useful.)

Increasing the population size rapidly is mandated in order to decrease the probability of extinction and to help reduce the potential for loss of rare alleles remaining in the population. It also helps during a transitional phase from outbreeding to inbreeding to increase the number of combinations of individuals that can be mated, a situation that will reduce the abruptness of the change warned against as "extreme inbreeding." Further, the rapid increase in population size also reduces the number of generations that will be vulnerable to inbreeding depression (see also Templeton 1980; Foose 1980; Frankel and Soule 1981). To accomplish this desired end, some innovative techniques have been used with success. Among these have been egg or embryo removal from a female of the targeted population and implantation into a surrogate mother of a foster species. How quickly the transition phase passes from outbreeding-adapted to inbreeding-adapted is dependent upon the amount of genetic variability remaining in the population (including that remaining in the individuals).

Healthy and inbred parents predispose their offspring to be healthy also. Therefore, individuals which are inbred but do not show any obvious deleterious manifestations of inbreeding are optimal choices for mates. The availability of such animals makes the transition faster and more efficient.

In their next step, Templeton and Read calculated the percentage contribution of each of the original founders to the present gene pool. They found that ideally, with 4 founders, each should have contributed 25% of the matings to the present-day gene pool. Such equalized contributions guard against loss of alleles, maintain heterozygosity, and therefore reduce exposure of genetic load and disruption of polygenes and over-dominance relationships between alleles. The authors calculated the inbreeding coefficient for each potential parent to select for high coefficient and good health. However, they did not recommend taking individuals with the most extreme inbreeding coefficients and mating these to each other first in order to speed the transition, as they may cause too abrupt a change, thereby increasing the probability of extinction.

In order to maximize the genetic variability of the offspring, Templeton and Read suggested selecting parents which, when mated, will produce the most even overall representation of the original founders (equivalent contributions of genome by percentage). Such results are accomplished most easily by picking parents with different ancestry (called disassortative mating with respect to pedigree). As Averhoff and Richardson (1976) and Templeton (1980) suggested, disassortative mating reduces the loss of alleles and maintains heterozygosity. It also prevents the acceleration of inbreeding at a harmful rate (see also Falconer 1981) that could cause both loss of alleles and negation of the adaptation (attempt) to inbreeding, as well as "transilience" (a condition in which rapid changes in traits may occur, producing undesired results). Thus, ideal mates that maximize genetic variability in the offspring are those that cause the offspring to bear alleles from all of the founders (stored in heterozygous condition resulting from the combination of gametes, and determined through the random assortment of alleles during meiosis when gametes are formed).

The last objective (but not the least in importance) is to slowly increase the inbreeding coefficient of the offspring. Thus, combinations resulting in non-inbred offspring as well as extremes of inbred offspring are avoided.

Two Notes on the Method

It is important to note that just because an individual carries deleterious alleles does not automatically mean that the entire genome is inferior. On the contrary, the individual may be carrying rare alleles that could be lost if it is excluded from the gene pool. By equalizing founder contributions, Templeton and Read (1983) alleviated this problem. However, there is no guarantee that this loss of rare alleles will not potentially occur. Adaptation to inbreeding is a treatment of last resort and addresses only the short-term hurdle of inbreeding depression.

In the "wild" the greater hurdle of adapting to rapid environmental changes cannot be solved with adaptation to inbreeding, alone. This is one of the lessons that the slugs _Arion_ and _Limax_ offer (Selander 1983). Long-term survival, in the face of today's intensity of selection pressures, requires something that maintains rare alleles and encourages the development of novel and beneficial alleles, a process that generally requires both luck and thousands if not millions of generations in nature.

SMALL POPULATIONS OF SELF-FERTILIZING AND POLYPLOID SPECIES

Selfing and (even number) polyploid species have a slightly easier task in adapting to colonizing situations (Selander 1983; Hamrick 1983; Clegg and Brown 1983), because the problem of mate selection and reproduction is reduced, even if population density and population size are very low (Selander 1983; Stebbins 1957; Baker 1959; Ghiselin 1969). A succession of bottlenecks after initial colonization (perhaps by a single individual) predisposes selection for the alleles determining self-fertilization. Species which typically inbreed (especially self-fertilizing species) do not experience the same level of "hybrid" vigor as outbreeding species that, having been inbred, are subsequently mated betwen lines. The fact that a population or species is adapted to self-fertilization or inbreeding suggests that advantages exist for populations that colonize readily with few individuals, sustain bottlenecks, are locally uniform, and store genetic variability between populations that may occasionally meet. Concurrent disadvantages also exist in that, while highly homozygous individuals or homozygous populations are very plastic, they are not easily adapted to sudden environmental or other selection changes and thus are extinction prone (Selander 1983). In other words, homogeneity of these species in new environments may favor survival and colonization, but when the environment changes suddenly, homogeneous colonizers are less able to adapt and may fail to survive.

One might suspect that highly inbred or selfing populations may not suffer from the repeated bottlenecks and habitat elimination in climatically stable areas such as the Hawaiian Islands. However, the drastic reduction of forest by humans, and the introduction of new diseases, parasites, predators, and depredators certainly have constituted severe environmental changes.

Restoration for self-fertilizing or polyploid species may be somewhat easier, however, than for diploid species. For plants, efforts with vegetational propagation, self-fertilization, and separation of individuals to found new lines, mimic an already successful agricultural and horticultural strategy. Highly inbred or selfing species usually have close relatives or other populations with which they are reproductively compatible (say, in captivity) or from which they were recently separated; for some, the gross morphological differences among subspecies, varieties or lines are in part a manifestation of phenotypic adjustments combined with sampling efforts derived from colonizations and subsequent bottlenecks. An option exists to ensure against the extinction proneness of syngenic lines, that is, to cross some lines to form new gene combinations that might withstand the new stresses; this risks, of course, the occurrence of heterosis (outbreeding depression). In addition, for these species, mixing of closely related varieties should not be discouraged as a last resort strategy to promote survival. Adapting species to manipulated changes in their genomes will be the new management challenge in endangered species restoration.

It is unfortunate that most of the applications of genetics to polyploid and self-fertilizing species are in agriculture, where selection is made narrow. In conservation, however, we hardly know what we should select. The formation of numerous lines and small populations throughout available habitat will allow nature to make its final choices in the face of change.

A THOUGHT ON ESSENTIALLY EXTINCT SPECIES

Schonewald-Cox, Baker, and Nakamura (in prep.) have proposed a means of closing the gap between inbreeding depression in small populations and adaptation demands addressed earlier for new and especially intense environmental stresses caused by human habitat modification. They assert that the techniques applied to the dusky sea-side sparrow (Ammospiza nigrescens) can be refined and adapted for island use with endemic species that are on the brink of extinction, specifically species that have close (genetically compatible) and traceable ancestors existing elsewhere. This, they assert, can be accomplished without necessarily interfering with the survival of the vanishing population remnant. The vanishing remnant could be treated simultaneously as Templeton and Read (1983) suggested. In a manner similar to what was done for the dusky sea-side sparrow (H. Kale, pers. comm.), semen is taken from one to several males of the endemic. The semen is used to inseminate females from various localities of the ancestral habitat, particularly areas where the ancestral species is successful in the face of modern human-related stresses. Efforts are made to not inseminate offspring with the same individual's semen that was used for the mother. The first generation offspring are (roughly) half of each, ancestor and endemic. In the next generation, the female offspring are 0.75 endemic and 0.25 ancestral. By the fourth generation, the offspring are 93.7% endemic and by the tenth generation they are 99.9% endemic. This is based on a simple and generalized manipulation:

$$\% \text{ endemic genome} = \frac{[(2^t) - 1]}{2^t} \times 100$$

(in which _t_ is the number of the backcross in the sequence). Note that the process becomes more complex if additional females are brought from new sources into the captive population. If females are selected from numerous habitats, different lineages can be tested for their environmental tolerances. This could help predetermine which individuals and their descendants might be potentially successful in different parts of the former range of the endemic species (in which the endemic can no longer survive). The developed (99.9% or more) endemic population(s) can be held until the natural population dies out and then used as a new founder, or it can be used to colonize other parts of the endemic's former range where natural selection can then determine whether this endemic with introduced (infused) alleles has a chance or not.

Once refined, such an approach could help bring back not only the vestiges of dwindling species, but it may offer nearly extinct species a chance to use modified niches with new vitality. Heterosis and other dangers of mixing 2 forms are risked, but this is done _ex situ_ and under controlled conditions. This is a more realistic approach than trying to adapt a dying species to the principal selection pressures of the past, or preserving (as opposed to conserving) a species adapted to selection pressures driving the species to extinction in the present. Needless to say, this is not the ultimate answer, but a step that has a potential to work some of the time for some of the species.

CONCLUSIONS: GENETICS, MINIMUM POPULATION SIZE, AND THE PROSPECT FOR HAWAIIAN SPECIES

The conservation problem of Hawai'i, fortunately, is one for which a great deal of specialized expertise is already available and interested. It may turn out that some aspect of genetic management for a few species may be one of several contemporaneous solutions. However, the conflict between species loss in the Hawaiian Islands, the highly specialized and complex niche relationships that Hawaiian endemics have developed, and economic development for an ensured profit may be irreconcilable.

Franklin (this volume) and also Frankel(1984), di Castri and Hadley (1984), and di Castri, Baker, and Hadley (1984) have spoken to the need for making additional habitat available, as have many others dealing with tropical and island extinctions. The Hawaiian Islands are the worst of all possible worlds in that many of the remaining passerines and plants not already extirpated by Polynesian deforestation are now endangered by current, continuing deforestation and other perturbations. The second wave of alien organisms that arrived with contemporary cultures only hastens the process. The theoretically obvious option of manipulating populations that remain, to adapt them to more generalized habits or marginal habitats, as well as to continued inbreeding, may prove inadequate for saving most of the remaining endemics. To restate what was said at the beginning of this paper, catastrophic changes are too rapid presently to allow species to naturally adapt. They even have trouble increasing in numbers, a baseline requirement for overcoming both external pressures and those derived from their own genomes. Certainly, for species that are still found in moderate numbers, as well as for species that are very close to extinction but with potential for recovery, the following steps should be considered.

First, determine whether the population is already isolated and adapted to inbreeding. If this is not known, survey the population's movements, including dispersal. Note the sources and destinations of dispersers, and measure their reproductive success. Isolation needs to be determined on both a short (single survey) and longer term (several years) level to determine whether apparent isolation or movement is, in fact, resulting in gene flow or inbreeding and isolation. It is important to determine even slight levels of gene flow. Even with high levels of inbreeding (see Wright 1978 and Chesser 1983), a very small amount of gene flow can be enough to prevent loss of rare alleles (an optimistic note).

Second, if the focal population is already adapted to inbreeding, then separate and isolate a number of small founder populations (as is feasible) throughout pockets of available habitat. Lines can be observed for their tolerance to marginal habitat conditions and placed accordingly. Namkoong (1983) had some suggestions on how this might be accomplished.

Third, if populations are not already adapted to inbreeding (i.e., their fecundity, survival, etc. are very low), then remove individuals and establish several small populations in captivity (for species that can survive in captivity). Inbred lines can be developed and subsequently released in isolated pockets to let nature take its course from there.

And, consider a fourth step of using controlled backcrossing to regenerate other populations in captivity or other habitats formerly occupied by the endemic species that have a potential to survive modern stresses.

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LITERATURE CITED

Allendorf, F.W. 1983. Isolation, gene flow, and genetic differentiation among populations. In Genetics and conservation, ed. C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde, and L. Thomas, 51-65. Menlo Park, Calif.: Benjamin Cummings, Inc.

Atkinson, I.A.E. 1977. A reassessment of factors, particularly *Rattus rattus* L., that influenced the decline of endemic forest birds in the Hawaiian Islands. Pac. Sci. 31(2):109-133.

Averhoff, W.W., and R.H. Richardson. 1976. Multiple pheromone system controlling mating in *Drosophila melanogaster*. Proc. Natl. Acad. Sci. U.S.A. 73: 591-593.

Baker, H.G. 1959. Reproductive methods as factors in speciation in flowering plants. Cold Spring Harbor 24th Symp. Quant. Biol., 171-191.

Ballou, J. 1983. Calculating inbreeding coefficients from pedigrees. In Genetics and conservation, ed. C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde, and L. Thomas, 509-520. Menlo Park, Calif.: Benjamin Cummings, Inc.

Beardmore, J.A. 1983. Extinction, survival, and genetic variation. In Genetics and conservation, ed. C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde, and L. Thomas, 125-151. Menlo Park, Calif.: Benjamin Cummings, Inc.

Benirschke, K. 1983. The impact of research on the propagation of endangered species in zoos. In Genetics and conservation, ed. C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde, and L. Thomas, 402-413. Menlo Park, Calif.: Benjamin Cummings, Inc.

Benirschke, K., B. Lasley, and O. Ryder. 1980. The technology of captive propagation. In Conservation biology, ed. M.E. Soule and B.A. Wilcox, 225-242. Sunderland, Mass.: Sinauer Assoc., Inc.

Carson, H.L. 1983. The genetics of the founder effect. In Genetics and conservation, ed. C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde, and L. Thomas, 189-200. Menlo Park, Calif.: Benjamin Cummings, Inc.

Chambers, S.M., and J.W. Bayless. 1983. Systematics, conservation and the measurement of genetic diversity. In Genetics and conservation, ed. C.M.

Schonewald-Cox, S.M. Chambers, B. MacBryde, and L. Thomas, 349-363. Menlo Park, Calif.: Benjamin Cummings, Inc.

Chesser, R.K. 1983. Isolation by distance: relationship to the management of genetic resources. In *Genetics and conservation*, ed. C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde, and L. Thomas, 66-77. Menlo Park, Calif.: Benjamin Cummings, Inc.

Clegg, M.T., and A.H.D. Brown. 1983. The founding of plant populations. In *Genetics and conservation*, ed. Schonewald-Cox, C.M., S.M. Chambers, B. MacBryde, and L. Thomas, 216-228. Menlo Park, Calif.: Benjamin Cummings, Inc.

Crow, J.F., and M. Kimura 1970. *An introduction to population genetics theory*. New York: Harper and Row.

di Castri, F., and M. Hadley. 1984. Making land management more scientific: experimenting and evaluating approaches. In *Ecology in practice. Part I, Ecosystem management*, ed. F. di Castri, F.W.G. Baker, and M. Hadley, 1-22. Paris: United Nations Educ., Sci., Cult. Org.

di Castri, F., F.W.G. Baker, and M. Hadley, eds. 1984. *Ecology in practice, Part I, Ecosystem management*. Paris: United Nations Educ., Sci., Cult. Org.

Falconer, D.S. 1981. *Introduction to quantitative genetics*. 2nd ed. London: Longmans.

Flesness, N., L. Grahm, and K. Hastings. 1982. *General information: International Species Inventory System [ISIS]*. Apple Valley, Minn.: Minnesota Zoo.

Foose, T. 1980. Demographic management of endangered species in captivity. *Internatl. Zoo Yearbook* 20: 154-165.

Foose, T. 1983. The relevance of captive populations to the conservation of biological diversity. In *Genetics and conservation*, ed. C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde, and L. Thomas, 374-401. Menlo Park, Calif.: Benjamin Cummings, Inc.

Frankel, O.H. 1984. Genetic diversity, ecosystem conservation and evolutionary responsibility. In *Ecology in practice. Part I, Ecosystem management*, ed. F. di Castri, F.W.G. Baker, and M. Hadley, 414-427. Paris: United Nations Educ., Sci., Cult. Org.

Frankel, O.H., and M.E. Soule. 1981. Conservation and evolution. Cambridge, England: Cambridge Univ. Pr.

Franklin, J.R. 1980. Evolutionary change in small populations. In Conservation biology, ed. M.E. Soule and B.A. Wilcox, 135-149. Sunderland, Mass.: Sinauer Assoc., Inc.

Futuyma, D.J. 1983. Interspecific interactions and the maintenance of genetic diversity. In Genetics and conservation, ed. C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde, and L. Thomas, 364-373. Menlo Park, Calif.: Benjamin Cummings, Inc.

Ghiselin, M.T. 1969. The evolution of hermaphroditism among animals. Quart. Rev. Biol. 44:189-208.

Hamrick, J.L. 1983. The distribution of genetic variation within and among natural plant populations. In Genetics and conservation, ed. C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde, and L. Thomas, 335-348. Menlo Park, Calif.: Benjamin Cummings, Inc.

James, H.F., and S.L. Olson. 1983. Flightless birds. Nat. Hist. 92(9):30-40.

Lasley, J.F. 1978. Genetics of livestock improvement, 3rd ed. Englewood Cliffs, New Jersey: Prentice-Hall.

Liu, E.H., and M.W. Godt. 1983. The differentiation of populations over short distances. In Genetics and conservation, ed. C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde, and L. Thomas, 78-95. Menlo Park, Calif.: Benjamin Cummings, Inc.

Namkoong, G. 1983. Preserving natural diversity. In Genetics and conservation, ed. C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde, and L. Thomas, 317-334. Menlo Park, Calif.: Benjamin Cummings, Inc.

Nei, M. 1975. Molecular population genetics and evolution. New York: American Elsevier.

Nei, M., T. Maruyama, and R. Chakraborty. 1975. The bottleneck effect and genetic variability in populations. Evolution 29:1-10.

Olson, S.L., and H.F. James. 1982a. Prodromus of the fossil avifauna of the Hawaiian Islands. Smithson. Contrib. Zool. 365.

Olson, S.L., and H.F. James. 1982b. Fossil birds from the Hawaiian Islands: evidence for wholesale extinction by man before Western contact. Science 217(4560):633-635.

Powell, J.R. 1983. Molecular approaches to studying founder effects. In Genetics and conservation, ed. C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde, and L. Thomas, 229-240. Menlo Park, Calif.: Benjamin Cummings, Inc.

Ralls, K., and J. Ballou. 1983. Extinction: lessons from zoos. In Genetics and conservation, ed. C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde, and L. Thomas, 164-184. Menlo Park, Calif.: Benjamin Cummings, Inc.

Ralls, K., K. Brugger, and J. Ballou. 1979. Inbreeding and juvenile mortality in small populations of ungulates. Science 206:1101-1103.

Schonewald-Cox, C., and J.W. Bayless. In prep. The boundary paradign: a geographic approach to an interdisciplinary problem in conservation. Natl. Park Serv., Univ. Calif. Coop. Natl. Park Resour. Stud. Unit, Davis.

Schonewald-Cox, C., R. Baker, and J. Bayless. In prep. Survival predispositions of elk restorations. Natl. Park Serv., Univ. Calif. Coop. Natl. Park Resour. Stud. Unit, Davis.

Schonewald-Cox, C., R. Baker, and R.M. Nakamura. In prep. An alternate approach to restoration of nearly extinct Hawaiian birds: a case study, Hawaiian crow. Natl. Park Serv., Univ. Calif. Coop. Natl. Park Resour. Stud. Unit, Davis.

Schonewald-Cox, C.M., S.M. Chambers, B. MacBryde, and L. Thomas, eds. 1983. Genetics and conservation. Menlo Park, Calif.: Benjamin Cummings, Inc.

Selander, R.K. 1983. Evolutionary consequences of inbreeding. In Genetics and conservation, ed. C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde, and L. Thomas, 201-215. Menlo Park, Calif.: Benjamin Cummings, Inc.

Shallenberger, R.J., ed. 1981. Hawaii's birds. 3rd ed. Honolulu: Hawaii Audubon Soc.

Soule, M.E. 1983. What do we really know about extinction? In Genetics and conservation, ed. C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde, and L.

Thomas, 111-124. Menlo Park, Calif.: Benjamin Cummings, Inc.

Soule, M.E., and B.A. Wilcox, eds. 1980. Conservation biology. Sunderland, Mass.: Sinauer Assoc., Inc.

Stebbins, G.L. 1957. Self-fertilization and population variability in the higher plants. Am. Nat. 91:337-354.

Templeton, A.R. 1980. A theory of speciation via the founder principle. Genetics 94:1011-1038.

Templeton, A.R., and B. Read. 1983. The elimination of inbreeding depression in a captive herd of Speke's gazelle. In Genetics and conservation, ed. C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde, and L. Thomas, 241-266. Menlo Park, Calif.: Benjamin Cummings Inc.

Wright, S. 1977-78. Evolution and the genetics of populations, Vols. 3 and 4. Chicago: Univ. Chicago Pr.

16.

DESIGN OF NATURAL AREA PRESERVES IN HAWAI'I

Jerry F. Franklin

ABSTRACT

Preserves, especially in Hawai'i, must be protectable and manageable. Elements in preserve design include defining objectives, determining minimal area requirements, identifying external threats, and identifying management activities to be conducted. Biological, economic, and social priorities must be considered. There is no substitute for detailed ecological knowledge and practical experience, but ecological compromises are essential. Land use on surrounding areas, successional processes, and life expectancies of preserves must be seriously considered, as well as special problems such as large or migratory animals. In Hawai'i, threats from introduced organisms, destruction and fragmentation of native ecosystems, and the abundance of rare taxa make decisions about preserve objectives and design especially critical. Intensive management of established preserves and accumulation of sufficient knowledge to accomplish this effectively and efficiently are crucial.

INTRODUCTION

The most challenging topic in natural area preservation is preserve design. The design of an area is the arena in which ecological knowledge is integrated with economic and social issues, and a project is developed that achieves not only the preservation objective but is practical. Acquisition and management issues must be considered as well as biological aspects of the preserve.

The challenge of preserve design extends to the scientist. What kind of area is required to protect the selected element(s)--size, shape, and habitat? Theoretical concepts, such as the theory of island biogeography (MacArthur and Wilson 1967) exist, but knowledge about ecosystems or the ecology of species in question is more critical to preserve design.

An ecologist's perspective on elements of preserve design for natural areas is the topic of this paper. Population biology and genetics contribute substantially to design, particularly where preserves are focused on threatened and endangered species, but this is covered by Schonewald-Cox (this volume). Aspects of design considered in this paper include size, shape, and ecological content and setting. Special preservation problems are identified, including those created by wide-ranging species and aquatic habitats. Difficulties unique to Hawai'i, for example, the number and scale of threats from alien species, are also discussed.

I regret that much of this paper is general and provides limited specific guidance for projects in Hawai'i. Unfortunately, guides almost always have to be general because of the diversity of preservation objectives, as well as differing biologic, economic, and social circumstances; ultimately, each project has a unique solution. There are, furthermore, not many preservation options in Hawai'i--potential reserve areas are limited in size and number. Some humility is also in order, since I am a mainlander advising a very competent group of island conservationists on how to do the job.

PRINCIPLES IN PRESERVE DESIGN

Steps in preserve design include definition of objectives, determination of area requirements (with consideration for disturbance patterns and succession), identification of external threats, identification of management activities, and design of a preserve unit that is protectable and manageable.

Definition of Preserve Objectives

The most important single principle in preserve design is identification of the objectives of the preserve, and the more precisely objectives can be defined, the better. What elements are the objects of the preservation effort? Is a specific organism to be protected, or an entire ecosystem? If the objective is related to preservation of a species, is the purpose to protect a viable population, a segment of a population, or a piece of critical habitat? If the objective is to preserve an ecosystem, is the objective to maintain a vignette of the present or some past condition, or is it to perpetuate the dynamics of the ecosystem and natural processes? This is a more difficult issue than it might seem. It is at the root of many discussions and disagreements on management objectives in national parks. In Hawai'i the importance of the time perspective has been highlighted by comparative analyses of the effects of Polynesian and Caucasian immigrations.

Inadequate definition of objectives has, in my opinion, caused more problems in design and management of preserves than any other single issue. On Federal lands the problem appears to result from a tendency to view preserves as static rather than dynamic ecosystems; major management problems, as well as drastic differences of opinion as to appropriate activities, often result. For The Nature Conservancy, the objective (often unstated) of simply preserving an attractive and available tract of land was a common, early problem and sometimes resulted in preserves of low ecological value or with unmanageable boundaries, or both.

Determination of Minimal Area

How large an area is required for a preserve? This is probably the question most frequently raised, whether by land managers, fund raisers, biologists, or the public. The answer varies because so many factors are involved--objectives of the preserve, ecology of the object elements, the nature of the surrounding landscape, and other factors.

In general, the preserve area must be large enough to encompass a viable biological unit. This may be defined as minimal population levels of a specific organism or a complete example (all trophic levels, perhaps) of an ecosystem. The size may be large, as is often the case with a forest, or may be quite small, as with some hot springs ecosystems. For whole ecosystems, areas are sought where modern human influences are minimized and a large array of natural processes is maintained.

Ecologists put their knowledge to work when determining the necessary size and shape of a preserve. Information on the natural history of the ecosytem or species in question is the most important part of this design effort. As mentioned, there are some ecological models that can be used to help quantify the size of area or size of population needed. Island biogeographic theory (MacArthur and Wilson 1967) is proposed as a basis for preserve design (Sullivan and Shaffer 1975), although many urge caution in use of an "insufficiently validated theory" (Simberloff and Abele 1976), and others warn against direct comparisons of island data and isolated patches of habitat on continents (Terborgh 1974). Other models make it possible to calculate distances required to eliminate external climatic influences on the interior environment of a forest stand. Home ranges of animals can be used to calculate the size of the reserve required; Sullivan and Shaffer (1975) provided some examples for predators, and Franklin and Trappe (1968) proposed a minimal size based on small mammal populations.

General models are no substitute, however, for extensive and accurate information on the ecological life history of a target organism or the structural and compositional patterns characteristic of an ecosystem. Knowledge of successional processes--paths and rates of change and the processes driving these changes--is essential but often lacking. Disturbances are an essential part of most ecosystems. What types, frequencies, and intensities of disturbance are characterized as "normal" or as catastrophic components of the ecosystem of concern?

The ecological analyses must also consider the current naturalness of the ecosystem in question as well as potential threats to that naturalness. What have been the effects of past human activities--for example, prevention of wildfire or introduction of alien organisms such as goats and pigs? What is the potential for additional unnatural impacts on organisms, processes, or structures characteristic of the ecosystem?

Some philosophical considerations make clear that the earlier comments on size are of limited usefulness; major compromises with the ideal are inevitably necessary. First, no area on earth is free of significant human influences. Modern man has caused changes everywhere. Second, it is rarely possible to have complete examples of an ecosystem. Major components have been effectively lost from ecosystems--for example, the passenger pigeon and American chestnut in the deciduous forests of eastern North America, and the buffalo from the shortgrass prairies. Hunting pressure and large home range requirements generally make it impossible to incorporate natural populations of larger mammals (ungulates or carnivores) in our preserves. Third, the scale of disturbances characteristic of many ecosystems in their primitive state generally cannot be accommodated in preserves. Catastrophic wildfire on the scale of thousands of acres and at intervals of several centuries is characteristic of the Douglas-fir forests of the Pacific Northwest. In these forests, minor disturbances that create compositional and structural diversity within the basic forest fabric (for example, bark beetles, root rots, and windthrow) can be incorporated within a preserve, but the prime catastrophe that resets these ecosystems requires a series of preserves and a patience with stochastic natural processes.

Most natural area preserves therefore involve major compromises. Varying degrees of human influences must be accepted, although designs can attempt to minimize this. On many Federal Research Natural Areas, natural populations of larger vertebrates have been written off. Hunting, fishing, and trapping are uncontrolled in U.S. Forest Service reserves and allowed but controlled in many U.S. Fish and Wildlife Service reserves. Ungulates and large predators are fully protected only in national parks, and even those areas may be under threat--witness the possible legalization of hunting Roosevelt elk in Olympic National Park, Washington, by native Americans. Similar compromises exist in many state areas and The Nature Conservancy reserves.

This is not to say that such compromises are necessarily fatal flaws in a preserve's design. Indeed, many ecosystems appear to function quite satisfactorily in the absence of ungulates or large carnivores. My objective is merely to point out that such compromises are inherent in most preserves and that puritanical posturing is, therefore, inappropriate. All reserves miss the ideal to at least some degree; it is a question of where the line for ecological compromise is drawn on a particular project.

Physical elements of size and shape are susceptible to analysis once preserve objectives are defined, ecology of the elements of interest are analyzed, and compromises with the ideal are accepted (explicitly or implicitly). The area must be large enough to essentially eliminate edge effects. It should be large enough to incorporate the patterns of structural diversity (for example, gaps) and compositional diversity characteristic of the ecosystem. The size should be sufficient to handle the natural disturbances inherent to the functioning ecosystem; an area sufficient to accommodate the disturbances that reset the ecosystem to an earlier successional state may be beyond possibility, as mentioned earlier.

The current or anticipated state of the lands surrounding the proposed reserve is a very important consideration in determining the size of the required tract. Will the reserve be an isolated tract in a matrix of ecologically contrasting lands? This can be a very critical issue when major structural contrasts are involved (e.g. between old-growth forest and clearcut lands) or when surrounding lands contain threats to organisms of interest (e.g. domestic pets may threaten some microtine or bird populations in a reserve located in an urban environment).

Buffers become particularly important when there are major contrasts or incompatibilities between preserves and surrounding lands. By maintaining an environment more compatible with preserve objectives, while still allowing a variety of other uses, buffers can provide transitions wherein undesirable influences of surrounding lands are diffused. Buffers can drastically reduce the area necessary within a preserve proper and may, in fact, be the only way to develop a design that is biologically, economically, and socially acceptable. Obviously, much larger preserves may be needed where circumstances dictate that any buffers must be included within the preserve, as many Federal land managers insist.

Some consideration of boundaries is necessary, as the topographic nature of reserve boundaries may overshadow the importance of size and shape alone. In mountainous regions, boundaries placed along major topographic breaks, such as ridge lines, can result in effective isolation of even small tracts from surrounding lands. By carefully selecting topographic boundaries, smaller viable reserves may be possible than if legal lines are selected as boundaries.

Complete watersheds are particularly advantageous as reserve units. They utilize topographic boundaries that are well defined in many landscapes. Watersheds have integrity as ecological units although some organisms may move in and out. They provide for fully protected aquatic ecosystems because the source areas for the surface water bodies are incorporated within the preserve. Watersheds also tend to incorporate considerable habitat diversity by their very nature (for example, the presence of environmental gradients of soil, topography, and elevation). Incorporation of habitat diversity may actually be a much more important criterion in the design of a preserve than its overall size.

<u>Management Programs</u>

The management program for a preserve is also an important consideration in preserve design. The preserve must be protectable and manageable, quite aside from considerations outlined in the previous section. Walt Matia, head of The Nature Conservancy's Stewardship Program, strongly emphasized this aspect of design in my discussions with him. For example, if prescribed fire is to be part of a management program, the preserve must be designed so that burns can be implemented; such programs may not be viable on a small, prairie preserve located in urban surroundings.

It is essential that the nature and intensity of management programs be identified during the design process. What activities will be necessary: burning, hunting, trapping, or grazing? What size and shape of preserve is necessary for the implementation of these activities?

Protection is a specific management element that must be considered even where no overt manipulative activities are planned. Are the boundaries identifiable? What is the risk of loss to destructive forces from outside the area? And how can this be minimized? Windthrow is a common threat, for example, in natural areas of large trees in the Pacific Northwest. The threat of blowdown can be minimized by considering patterns of storm winds and selecting windfirm topographic locations for boundaries.

In all cases, preserve design must incorporate specific considerations of proposed management activities and the size and shape necessary for the implementation of those activities.

SPECIAL PROBLEMS IN PRESERVE DESIGN

Large and Migratory Animals

Animals that are large or migratory, or both, present special problems in preservation that are generally not appropriately handled in the context of strict nature preserves or Research Natural Areas. Many ungulates, top carnivores, birds, and marine mammals are among those that present problems (see Terborgh (1974) for examples). The role of preserves with such animals is generally confined to protection of key habitats for breeding, migration, or wintering. Such preserves are generally only effective in the context of comprehensive management programs (for example, those developed by the U.S. Fish and Wildlife Service for threatened or endangered species). These programs typically involve management of the animals throughout their ranges and on all types of lands, and even international agreements. Natural populations of ungulates and predators are sometimes protected in national parks although even parks may lack sufficient size for some species. Restrictions on hunting in parks are also under increasing pressure, and changes in rules could further reduce locales for studying unhunted populations of many species.

Any preserve for large or wide-ranging animals must fit into the context of a larger species conservation effort to be effective. Natural area preserves will generally play limited, although sometimes critical, roles. Simply preserving such species may tax human society, let alone maintaining natural populations of such species.

Aquatic Ecosystems

Preserve design for aquatic ecosystems or organisms can be very difficult. The watersheds of these ecosystems would ideally be included in a preserve so that a natural hydrologic regime could be maintained along with the chemical and physical properties of the water itself. This is sometimes possible with streams, ponds, and other relatively small aquatic features. In reality, such control is rarely possible with larger aquatic ecosystems--rivers, large lakes, and estuaries. Our larger national parks and wilderness areas provide us with the few significant natural examples of such types. Even in these cases some external influences can still significantly modify natural conditions --for example, acid rain in the case of poorly buffered lakes and ponds.

An alternative to direct control is to have all or part of the watershed or source area for the aquatic ecosystem managed under a regime consistent with the preservation objectives. This may prove to be the most desirable approach (economically, socially, or both), even when complete watershed control is feasible. This may mean having a part of the watershed within a less restrictive conservation category (for example, a park) or even dedicated to a consumptive but compatible use, such as production of water for a municipality or irrigation district. The key is to develop cooperative management programs for watersheds that will insure the integrity of the water supply for aquatic ecosystems. Hawai'i is pioneering in these approaches.

Another essential design element for aquatic preserves appears to be direct control of the aquatic habitat and the immediate environs. Preservation objectives can often be at least partially achieved with control of only the water body and adjacent shores; this may mean a lake, pond, marsh, or a reach of river or stream and the adjacent terrestrial areas. The objective is the control of the interface between land and water, particularly where major interactions or transfers between land and water are occurring. Examples of such interactions include overland flows of water, provision of protective cover and litter by riparian plants, and transfer of woody debris to the aquatic ecosystem.

Succession

Preservation of some ecosystems is simply not possible in the narrow sense of perpetuating a community of a given composition or structure because of successional processes. We tend to think of an ecosystem as being in a dynamic equilibrium with an environment, including the disturbance regime. A sere is initiated by a catastrophic event, proceeds through a series of ecological stages (often differing in composition, structure, and cycling processes), and is eventually reset to an initial condition by another disturbance episode, with the pattern repeating ad infinitum. This is a simple but useful general model for many combinations of ecosystems and disturbance regimes.

Ecosystems representative of primary succession (that is, developing on freshly created surfaces) often cannot be maintained. Such ecosystems are the consequence of unique events--a volcanic eruption or glacial retreat--that cannot be readily duplicated by humans. Such seres can only be understood and allowed to proceed with minimal human interference. Examples of such ecosystems are not always obvious at first glance. A good example may be some of the 'ohi'a (Metrosideros polymorpha) forests in Hawai'i, a topic discussed in detail by Mueller-Dombois (this volume). Some of these forests are a consequence of an episode of vulcanism that provided conditions suitable for their establishment. The forests have developed, site conditions have been altered, and senescence has occurred. Development of forests of similar structure may have to await another volcanic eruption. Similar circumstances may exist with Metrosideros forests that have developed on tephra soils in New Zealand.

The point in preserve design and management is to recognize that there may be situations where ecosystems cannot be maintained, even with human intervention. There are other circumstances that also produce this result--for example, where relict communities or organisms are encountered that are no longer capable of regenerating themselves on a site. We need to be aware of these limitations.

Life Expectancies and Risk Spreading

There is relatively little basis, as far as I know, for judging life expectancies of preserves of any size, but some observations may be useful:

1. Most losses of preserves have been a consequence of social, not physical, processes.
2. Losses of Federal preserves have tended to be inversely related to difficulty of establishment; for example, congressionally established areas (national parks, wilderness areas) have been quite stable while Research Natural Areas (which are established by agency regulations) have varied depending upon agency commitment and the complexity of their establishment process.
3. Losses of The Nature Conservancy preserves have most often been the result of an upgrading process and reflect poor initial selection or design, or both.
4. Erosion of natural ecological values rather than outright loss of preserves has been most common.

One issue in the design of preserve systems has been the relative merit of few larger or many smaller preserves. Strong cases have been made in the scientific literature for the importance of large preserves, particularly by individuals interested in larger vertebrates (Sullivan and Shaffer 1975). As a plant scientist I have tended to favor smaller and more widely dispersed preserves.

Any overall conservation strategy obviously must and will include a range of sizes. Large areas are clearly essential to some objectives, as already noted. It would be imprudent to put all of our conservation eggs into a very few baskets, however, if we don't have to. A series of smaller areas has the particular advantage of reducing the danger of loss; that is, it spreads the risk. This can also be a genetically advantageous strategy by incorporating greater genetic diversity of many organisms. I have strongly favored a series of modest Research Natural Areas for Douglas-fir (Pseudotsuga menzesii) in the Pacific Northwest over 1 or 2 large tracts to incorporate more of the geographic and genetic variability and to reduce the chance of losing a large proportion of the reserved forests to a single catastrophe.

Fortunately, the strategies of a few large versus many small reserves are rarely mutually exclusive. Where conflicts do arise theoretical models will not substitute for judgment and prudence in the decision process.

PRESERVE DESIGN IN HAWAI'I

Hawai'i presents some incredibly difficult problems in preserve design, as many people already know. The first problem is the limited acreage of unmodified landscape--a problem that is not unique to Hawai'i. Much of Hawai'i has been converted to various human uses including recreation, urban and military developments, and agricultural production. Habitat destruction limits the possibilities for natural area preservation at the outset, especially at low elevations where almost no unmodified ecosystems exist.

Alien organisms are a huge and pervasive obstacle to preserving Hawai'i's natural diversity. Smith (this volume) estimates that there are 600 naturalized plants in Hawai'i, of which 86 are pests. Some of these plants, such as banana poka (Passiflora mollissima), strawberry guava (Psidium cattleianum), fire tree (Myrica faya), and Andropogon and other grasses, are very aggressive and readily displace native plants. Introduced animals include such conspicuous organisms as feral goats (Capra hircus), pigs (Sus scrofa), and feral sheep (*Ovis aries*) and the mongoose (*Herpestes auropunctatus*), as well as numerous less conspicuous animal species. Some of these animals function as vectors for alien plants while others prey directly on native fauna. Introduced diseases, such as avian malaria, have had major impacts on some groups of animals. Alien invertebrates continue to establish themselves and are having serious impacts on native insects and mollusks; some also serve as disease vectors.

Irreversible changes in Hawaiian ecosystems have resulted from the combined effects of ecosystem disturbance, introductions of alien organisms, and extinction of native organisms. For example, 120 native plants (11% of the flora) are known to be already extinct (Wagner, Herbst, and Yee, this volume). Environmental conditions (fire and soil hydrologic and nutrient regimes) have been drastically, and perhaps permanently, altered by alien organisms (Smith, this volume). It is, therefore, simply not possible to recreate complete examples of some ecosystems. It will also be extremely difficult to protect examples of some ecosystems from the continuing onslaught of aliens.

Ecosystems in Hawai'i are threatened in ways, and on a scale, that are beyond any in my North American experience. Entire ecosystems, not merely species or trophic levels, are threatened with extinction. Furthermore, such drastic potentials exist in the absence of any additional human disturbance. In many areas of the world, undisturbed ecosystems are resistant to the invasions of aliens; for example, Eurasian annual grasses will generally not replace native bunchgrasses in the steppes of the Pacific Northwest unless these ecosystems are disturbed by grazing. This is clearly not the case in much of Hawai'i where human intervention is essential to protect even undisturbed native ecosystems from aliens. The threat of banana poka exemplifies for me the ultimate nightmare--an alien species that is capable of invading intact rain forests and completely destroying them.

The excellent general scientific data base for the Hawaiian Islands is favorable to preservation efforts. Thanks to the efforts of many individuals and, especially, the Endangered Hawaiian Forest Bird Project, we have a good understanding of where key tracts of land are located, as well as the overall status of ecosystems and many species.

Conservation Triage

A critical step in preservation of Hawai'i's natural diversity would appear to be some decisions about overall objectives--a conservation triage. What should be the relative emphasis on ecosystems versus species?

The huge numbers of threatened and endangered species have been mentioned by several symposium speakers. How much effort should go toward keeping "basket cases" in existence? Is it better to focus on preservation of biological structures and processes (including evolutionary processes) as represented by the ecosystems? Or, should we increase preservation of some components --specific species? A sound system of ecosystem-oriented preserves will take care of many species, including species currently unknown to us. On the other hand, species are valuable as indicators and components of ecosystems and as rallying points for public conservation efforts, as well as having an intrinsic worth.

Another triage issue is purity versus practicality in preserve selection and design. As Holt and Fox (this volume) have suggested, emphasis may need to be on preserving the "best" available areas of specific ecosystems.

In this objective setting and in triage, as well as in carrying forward the actual preservation efforts, it is absolutely essential that the small community of scientists and land managers in Hawai'i cooperate. Continuing conflicts will ensure that the preservation effort will fall far short of its potential and need. A common front will make the need and priorities clear to the public and to the politicians. A fragmented scientific community and lack of long-range land use planning will confuse the issues and make it easy for opponents to defeat preservation efforts.

Acquisition and Intensive Management

The circumstances in Hawai'i necessitate new and creative solutions to preserve design, as biological issues are combined with the social and economic realities of land acquisition. Some new approaches to conservation problems have already been taken. The acquisition of conservation easements and development of cooperative management agreements on target lands and in buffer areas are good examples. Where but in Hawai'i would someone conceive of purchasing the right to be managerially responsible for someone else's watershed? With land ownership such a controversial issue in Hawai'i, it might be possible to arrive at long-term agreements with owners of critical conservation properties, agreeing to preservation in return for rights to use noncritical lands elsewhere.

Intensive management efforts are an overwhelmingly critical element of natural area preservation in Hawai'i--the "active management program" of Holt and Fox (this volume). Identification of problems and selection of management strategies have to be early and integral parts of preserve design--much more than is often the case with mainland preserves. It is obvious from the planning and resources that are going into the management programs on several of the new Nature Conservancy preserves, that this is known. I view Hawai'i as a leader in the field of active (versus passive) management of natural areas; things cannot simply be left alone, not even for short periods. Mainlanders have much to learn in this regard in natural area management.

Intensive management will take many forms, including activities to eliminate or control aliens, to reconstruct ecosystems, and to perpetuate processes. Some approaches to the eradication or control of alien species are fencing, hunting and trapping of animals; introduction of insects or diseases for biocontrol of plants; and mechanical or chemical removal of plants. L.L. Loope (pers. comm.) suggested that feral animal control appears the minimum management required for any land dedicated to preservation of natural communities of native biota in Hawai'i. Forest structures and compositions can be reestablished in efforts to reconstruct functional ecosystems. Silvicultural practices such as planting, thinning, and killing of trees (to create dead wood structures) may be appropriate. (Efforts to reconstruct natural forests on cutover lands in Redwood National Park, California, provide an example.) Scott, Kepler, and Sincock (this volume) have suggested activities that can be used to perpetuate natural reproductive, migratory, and selective processes --transplantation of organisms, manipulation of organisms in the wild, and captive propagation. Simulation of disturbance regimes is another managerial approach to perpetuating natural processes. Prescribed fire management is a typical activity on the Mainland, and some day simulating the effects of flooding on segments of floodplain communities along dam-tamed rivers may be done. Are there similar processes that need to be perpetuated or simulated in Hawaiian ecosystems? Could you imagine attempting to simulate the effects of a volcanic eruption?

In any case, the management programs will be as complex and sophisticated as those on intensively managed agricultural and forest lands. Small natural areas may receive the management attention currently given only to national parks. Dollars, trained personnel, and knowledge will be essential to these programs. More knowledge of the species and the ecosystems will be especially critical in order to design and monitor management activities. All parties--agencies, universities, The Nature Conservancy, and other groups --have to drastically increase efforts at generating the necessary information.

Such intensive management of natural areas I find both a scary and a humbling prospect. Scary, because we are more and more assuming a God-like role, carrying the burden of perpetuating ever-increasing numbers of ecosystems and species, presumably forever. It reminds me of the responsibilities mankind has assumed for safe storage of long-lived nuclear wastes. Humbling, because of the limited knowledge available for carrying out our tasks. I am convinced that we know a lot less about ecosystem structure and function than we think. As I recall the level of understanding that we had of old-growth coniferous forests in the Pacific Northwest just 15 years ago, I am amazed at how little we saw of what was before us. And how confident we were that we knew almost everything of importance! At that time no one suspected that over 50% of the energy produced by these forests typically goes into maintaining the below-ground portions of the ecosystems. No one knew that microbes in rotting wood are fixing significant quantities of nitrogen, or that non-growing season photosynthesis could constitute half or more than half of the yearly production on some sites. The examples could go on ad infinitum. My point is that we scientists and resource managers should repeat statements of fallibility to ourselves nightly, lest we begin to believe that our limited understanding of ecosystems is complete, let alone represents "truth."

Preserve design in Hawai'i will often require original approaches to landscape control and intensive management programs. Objectives must be well defined and prominent as various design alternatives and management strategies are considered. Land acquisition and passive management cannot substitute for clarity of purpose, as often seems to be the case on the Mainland.

CONCLUSIONS

Preserve design is a process that involves ecological, social, and economic considerations. Definition of objectives is paramount in both design and management of preserves. Sound scientific information on the ecosystems and organisms of interest is essential; ecological theory is no substitute for such knowledge. Any guidelines on size, shape, and other criteria must, of necessity, be general as each design problem is unique.

Preserve design in Hawai'i presents the most difficult problems because of pervasive disturbance, an abundance of aggressive and influential aliens, land-use conflicts, and land ownership issues. Solutions will require many and original alternatives to outright acquisition, such as purchase of easements and use of buffers with compatible land uses. Intensive management programs will be necessary because passive management will typically not preserve the elements of interest.

LITERATURE CITED

Franklin, J.F., and J.M. Trappe. 1968. Natural areas: needs, concepts, and criteria. J. For. 66:456-461.

Holt, A., and B. Fox. Protection status of the native Hawaiian biota. [This volume]

MacArthur, R.H., and E.O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Monogr. Pop. Biol. 1.

Mueller-Dombois, D. Ohia dieback and protection management of the Hawaiian rain forest. [This volume]

Schonewald-Cox, C. Genetics, minimum population size, and the island preserve. [This volume]

Scott, J.M., C.B. Kepler, and J.L. Sincock. Distribution and abundance of Hawaii's endemic land birds: conservation and management strategies. [This volume]

Simberloff, D.S., and L.G. Abele. 1976. Island biogeography theory and conservation practice. Science 191:285-286.

Smith, C.W. Impact of alien plants on Hawaii's native biota. [This volume]

Sullivan, A.L., and M.L. Shaffer. 1975. Biogeography of the megazoo. Science 189:13-17.

Terborgh, J. 1974. Preservation of natural diversity: the problem of extinction prone species. BioScience 24:715-722.

Wagner, W.L., D.R. Herbst, and R.S.N. Yee. Status of the native flowering plants of the Hawaiian Islands. [This volume]

17.

ECOSYSTEM MONITORING, RESTORATION, AND MANAGEMENT IN HAWAI'I: A SUMMARY

Sheila Conant

The speakers in this session dealt with practical and philosophical approaches to the protection and management of Hawaiian ecosystems. Problems in monitoring and restoring ecosystems were considered; allowances for fundamental natural processes such as succession, cohort senescence, gene transfer and bottlenecks, and natural selection were discussed; and the immense problem of preserve design in the light of minimum population size, genetics, and other biological, sociological and economic constraints was considered. The need for more knowledge is apparent in all of these areas, but the demand for directed action to preserve what remains is immediate.

MONITORING WITH EXCLOSURES

Exclosure studies have been and will continue to be a very important method of monitoring ecosystem restoration and management. Such studies have helped in determining and demonstrating impacts of feral ungulates and, in some cases, non-native plants. Loope and Scowcroft encouraged continuation of exclosure research and pointed out the importance of timely publication of results.

The recovery potential of a number of native ecosystems has been clearly demonstrated by the results of exclosure studies. In other cases the existence of such potential is unclear, due either to a lack of data or to the fact that available data do not clearly show that recovery potential exists. For example, ecosystem recovery has been good in some rain forest exclosures, poor in others. It is clear that exclosure studies should continue for 2 reasons. First, some ecosystems have not been studied at all; and, second, more time is needed to monitor ecosystem response in existing exclosures.

In addition to demonstrating potential for ecosystem response, exclosure studies provide ungulate-free areas in which experiments may be conducted. They also provide areas in which non-native plants can be successfully controlled. The success of exclosures for preventing the extinction of species, particularly plants, also has definite possibilities. The authors emphasized the need for careful planning in this regard.

Exclosures can be particularly valuable if constructed before alien plants invade and before feral ungulate damage becomes severe. Management and control of alien plants and animals within exclosures is usually a necessary adjunct to using exclosures to protect ecosystems from disturbance.

'OHI'A DIEBACK

Mueller-Dombois presented a comprehensive summary of the 'ohi'a (Metrosideros polymorpha) dieback phenomenon, including a review of previous research results dealing with types and characteristics of dieback. Potential causes of dieback currently under investigation were identified and included climatic instability, soil and stand factors.

The results of 'ohi'a dieback research have some important and interesting implications for preserve design, management and our understanding of 'ohi'a forest ecology. Because dieback occurs in mosaics, 'ohi'a forest preserves must encompass stands made up of a spectrum of different life stages of 'ohi'a. Such preserves, which would have to be large, would accommodate the dieback process itself. Results of dieback research clearly show that there is no need to replace dying trees because they are actually in the process of replacing themselves. Dieback appears to be a natural successional process rather than a symptom of disturbance or poor health. Different forms of 'ohi'a are adapted to different conditions and naturally replace forests in different stages or areas. 'Ohi'a dieback cannot be successfully stopped by soil fertilization, and attempts to do so are likely to encourage the abundant growth of alien plants otherwise ill-adapted to dieback soil conditions.

Mueller-Dombois mentioned 3 areas where further research could contribute to the understanding of dieback in relation to preserve design and management. First, there is a need for complete mapping of physical habitat types. Second, studies are needed to elucidate the effects of dieback on rare plants. Finally, scientists need to have a better understanding of the effect of dieback on alien plants.

In conclusion the author stressed that effective preserve design aimed at the conservation of 'ohi'a forests must recognize that 'ohi'a dieback is a dynamic geographic process and, consequently, adequate size and strategic distribution are very important considerations in the design of rain forest preserves.

ECOSYSTEM RESTORATION

One of the most difficult aspects of ecosystem restoration in Hawai'i is the definition of goals, that is, establishing a clear description of what constitutes a restored ecosystem. The principal reason for this difficulty is that scientists and managers lack information about what ecosystems were actually like in their natural or near-natural state. Another major problem is posed by the ecosystems themselves, inasmuch as they are constantly changing: individual species are evolving, natural and artifactual loss and recruitment of species are ongoing, succession is continuing, and long-term ecological changes are inevitable.

In spite of these difficulties most scientists, managers, and others agree that ecosystem restoration is desirable. Perhaps the most appropriate goals of this process are the retention and restoration of genetically and ecologically diverse entities. Results of ecosystem restoration have been varied. For example, human attempts at the restoration of habitat on Laysan Island seem to have had little effect: the ecosystems largely recovered from disturbance on their own. On the other hand, exclosure studies show that fencing to exclude feral ungulates may have a significant positive effect on the restoration process in some ecosystems. In other cases, it is too soon to tell whether or not human intervention has aided in the restoration process, and in a few cases, for example, that of the nene (Nesochen sandvicensis), human efforts to date have not been entirely successful.

There have been almost no cost-benefit analyses of ecosystem restoration in Hawai'i. While some may consider this a disadvantage, unique ecosystems and their component elements have intrinsic values that are difficult to quantify. Placing dollar values on the benefits of restoration encourages the thought that some alternative use of the ecosystems may provide more financial gain and is therefore better. Such reasoning, if applied to watersheds for example, could be ecologically disastrous.

Lamoureux's recommendations reinforce those of previous speakers in the Symposium as well as years of research on the topic. Alien herbivores and aggressive plants should be removed and kept out of ecosystems we are attempting to restore. Replanting and restocking should be carried out with genetically similar forms or species. Finally, to the extent possible, detrimental changes should be anticipated and stopped or arrested before, during, and after programs for ecosystem restoration are conducted.

PRESERVE DESIGN: GENETICS AND POPULATION SIZE

Schonewald-Cox indicated that conservation may have several different objectives, for example, the conservation of species, the conservation of genetic variability, or the conservation of ecosystems and their life processes. Conservation of ecosystem processes is the objective of many, though not all, natural preserves being designed today.

A number of limitations should be acknowledged regarding the preservation of genetic and ecological diversity:

1. For the most part, sizes of protected habitats will not increase significantly in the world, although the effectiveness with which they are protected may increase.
2. There will continue to be increased pressure from the human population for resource use, space, etc.
3. The contrasts that exist or seem bound to occur between natural preserves and land uses outside of them are likely to evoke boundary and land use disputes.
4. Most rare species will never exceed their minimum effective population size (i.e., self-sustaining population size) in our lifetimes. Therefore it is worthwhile to attempt to establish self-sustaining ecosystems.

In choosing species for consideration for artificial propagation, one must ask the question, what is a small population? The answer cannot be described solely in terms of numbers but must be based on how genetic diversity is manifested and maintained. If there is too little natural genetic variability present to allow the population (regardless of its size) to adapt to changes, then the population is too small. Such populations are highly vulnerable to extinction.

In Hawai'i, many species populations are naturally small, having evolved from small founder populations, so that small population size is not necessarily a disadvantage. Such species may already be adapted to inbreeding, that condition regarded until recently as one of the most severe roadblocks to successful artificial propagation programs. Recent research, for example that accomplished by Templeton on the Speke's gazelle

(Gazella spekei), has shown that even in species where inbreeding depression can be a problem, it can be solved by a breeding program aimed at adapting the captive population to inbreeding itself.

The author made several recommendations regarding the management of species close to extinction but which still have some chance of recovery:

1. Determine whether the population is adapted to inbreeding.
2. If the population is adapted to inbreeding, separate and isolate several small founder populations in available habitat and allow them (with appropriate management, if necessary) to increase.
3. If the population is not adapted to inbreeding, establish a captive propagation program using several different populations. When enough plants or animals have been produced, release the inbred lines into suitable habitats.

These recommendations are aimed at establishing or allowing to exist, populations that are adapted to being small in size, even if they were not naturally so to begin with. Such adaptation should increase the chances of survival.

PRESERVE DESIGN: SIZE, SHAPE, AND DISTRIBUTION

There are some very special problems of preserve design in Hawai'i. For example, many Hawaiian ecosystems are very limited in size, especially at low elevations. The problem of alien organisms is tremendous and pervasive. Unfortunately, the fact that irreversible changes have occurred in some ecosystems renders it impossible to restore some and difficult at best to protect others.

Franklin suggested that although ecological theories and models may provide guidelines for preserve design, they have their limits. In many cases good ecological studies and basic natural history are equally, if not more, important in preserve design and management. Common sense and intuition are usually of great importance also. In this regard scientists and managers must acknowledge economic and social considerations to be successful conservationists.

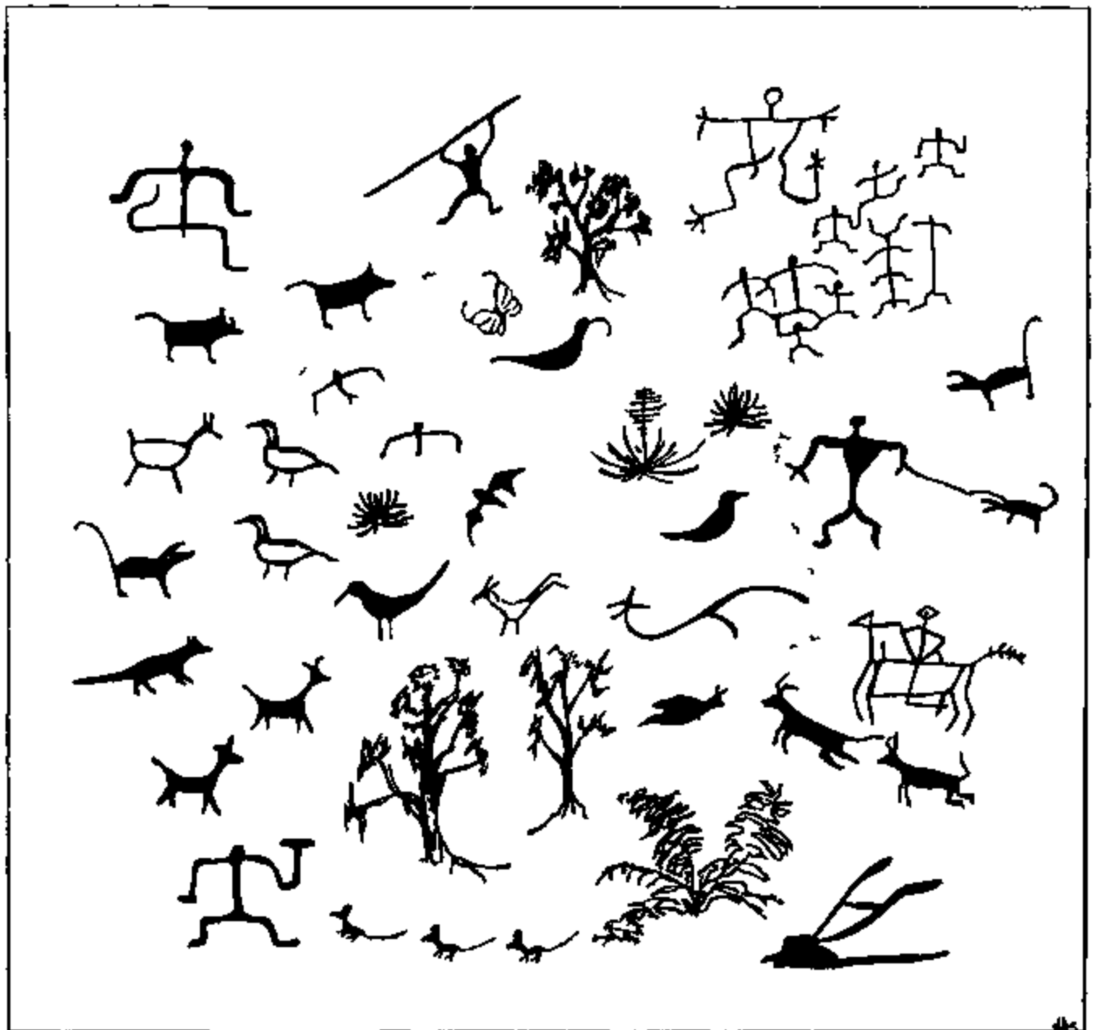
Although conservation problems in Hawai'i are considerable, a number of positive factors exist. There are many individuals and institutions sincerely committed to conservation. Hawai'i already has an initial set of preserves in the form of natural areas, national parks, wilderness areas, etc. Our scientific data base, though not complete, is of high quality, in some respects.

Specific recommendations regarding preserve design and management seem clear. It will be necessary to apply triage strategy to preserve design. It is simply not possible to attempt to conserve all remaining ecosystem types, and a system of priorities should be developed without delay. Establishment of regional programs for preserves should help in the overall planning process. Although the preservation of ecosystems is an excellent goal, management aimed at the preservation of individual species should not be neglected. Species, especially those of a charismatic nature, may serve as rallying points for the public, may be prized for their intrinsic value, or may be important ecological indicators.

Intensive management efforts are extremely critical. The control of alien plants and animals must be a part of any successful preserve program. In this regard Hawai'i should be a leader in the area of ecosystem restoration because we do not have the choice of simply leaving things alone and hoping they will recover without any efforts to remove the initial cause of disturbance. The inclusion of extensive buffer areas at the perimeters of some preserves is an effective management tool.

To effectively conserve ecosystems, scientists and managers must deal with realities in the socioeconomic realm. Public opinion, political aspects of conservation issues, efforts at compromise and the like, all play an important role in successful implementation of ecosystem preservation and management programs. In this regard, large private land owners may be much more willing to commit themselves to conserving native ecosystems or species if they are compensated with rights to use of public lands or other suitable trade-offs.

IV. ROLES OF RESPONSIBLE GROUPS



18.

CURRENT AND FUTURE ROLES OF AGENCIES, CONSERVATION GROUPS, LEGISLATURE, AND THE PUBLIC IN PRESERVING AND MANAGING HAWAIIAN ECOSYSTEMS: A SUMMARY

Cameron B. Kepler

The first 3 sessions of this symposium detailed the tremendous variety of stresses to native ecosystems that interact synergistically to the detriment of Hawai'i's flora and fauna. There are also many interacting people and agencies representing political and social perspectives, often at apparent odds with each other and with Hawai'i's natural resources. Solutions to our biological problems invariably involve interactions among groups holding very diverse points of view, and both the biological and political realities of a given situation must be considered if we are to succeed in protecting our natural heritage. Some of the human concerns and goals for the environment were expressed through a variety of agencies and citizen groups in a separate session of this Symposium. Participants and groups represented included: P. Stine, Fish and Wildlife Service; K. Taketa, The Nature Conservancy; B. Harry, National Park Service; C. Lamoureux, Conservation Groups; L. Landgraf, Department of Land and Natural Resources; A. Chang, Government; H.P. L'Orange, Private Landowners; S. Conant, Biologists; and P. Desha, Office of Hawaiian Affairs. These concerns are here reviewed and commented upon.

THE U.S. FISH AND WILDLIFE SERVICE

The U.S. Fish and Wildlife Service (FWS) is attempting to protect land critical to the needs of wildlife in Hawai'i, consistent with legislation and goals of the many recovery plans for Hawaiian species. The agency has been successful in safeguarding habitat for 18 species of seabirds in the Northwest Hawaiian Islands, and for the many endangered species also found there. FWS has developed 5 wildlife refuges totalling 500 ha for endangered waterbirds on the main islands, and is moving to acquire additional wetlands identified in the Hawai'i Waterbird Recovery Plan (Walker et al. 1977). If Kealia Pond on Maui and a few small wetlands on Hawai'i can be secured, this refuge system will then embrace all the major islands and provide adequate security for Hawai'i's endangered waterbirds. Kealia Pond is particularly important, for it is the largest remaining unprotected wetland in the main islands, and at times holds over one-third of Hawai'i's endangered black-necked stilt (Himantopus mexicanus knudsoni) population.

The FWS does not currently own any forest bird habitat. This is regrettable. However, FWS is pursuing a Big Island project in upper Hamakua that could protect forest bird habitat identified as crucial for the Hawaiian hawk (Buteo solitarius), 'akiapola'au (Hemignathus munroi), Hawai'i creeper (Oreomystis mana), Hawai'i akepa (Loxops coccineus), and 'o'u (Psittirostra psittacea).

FWS research on endangered species is a continuing effort. Using the results of the Hawai'i Forest Bird Survey (Scott et al., in press) as a base, research is focusing on the relative importance of those factors presently limiting the distribution and abundance of some of the most critically threatened bird species. It is hoped that this program can be coordinated with the efforts of others in Hawai'i to produce a truly multi-disciplinary effect. An integrated research program on the effects of disease, ungulates, predators, arthropods, and habitat quality does not imply that we lack the knowledge to begin managing land already legally protected. FWS should encourage public agencies responsible for natural ecosystems to manage their land for its intrinsic natural values.

THE NATURE CONSERVANCY

Almost all of us are familiar with The Nature Conservancy (TNC) and its successful forest bird program. It has brought more than $6,000,000 into the State and acquired 4 important preserves, totalling in excess of 48 km^2 on Kaua'i, Moloka'i, Maui, and Hawai'i. TNC has launched a Heritage Program to compile up-to-date data on the distribution of endangered plants, animals, and communities. In so doing, it is providing a vehicle for ascertaining the natural value of lands everywhere in Hawai'i. Published as well as unpublished information is being used to build the systems database. This means that research biologists for the first time can deposit data on the distribution of endangered taxa in a program that will be increasingly utilized in the decision-making process. The time is fast approaching when land managers and developers will no longer be able to remain ignorant of natural resource values in their decisions.

As successful as these programs have been, they are not in themselves TNC's only important accomplishments. The organization has provided an outstanding service in promoting interaction among diverse segments of the Hawaiian community. This is one of TNC's greatest strengths and accounts for its success in acquiring Kamakou and Waikamoi Preserves. TNC has brought State and Federal land managers and biologists into a close forum with businessmen and established corporate families to approach conservation in Hawai'i in a pragmatic, positive fashion. This has resulted in a significant broadening of the conservation base, funnelled financial support from Hawai'i's business sector into important conservation projects, and spread a conservation message into corporate boardrooms in a highly effective manner. The ensuing dynamic interaction will benefit resource programs far into the future.

NATIONAL PARK SERVICE

The National Park Service (NPS) controls over 1036 km^2 or 5% of the land in Hawai'i and clearly must continue to play a major role in protecting our natural resources. It has steadily moved from the posture of simple protection to active management and, with research biologists and management staff stationed in Haleakala (HALE) and Hawai'i Volcanoes (HAVO) National Parks, is increasing our understanding of what needs to be protected while simultaneously inventing or improving the management tools needed to move the parks from disturbed to pristine ecosystems. The successes in removing feral goats (Capra hircus) and, more recently, eliminating feral pigs (Sus scrofa) from relatively large management units in HAVO, generates optimism that similar control efforts will work at HALE. The current effort to fence the entire Crater at HALE appears to be heading for success and will for the first time allow Park personnel to eliminate goats within the Crater and provide for the regeneration of alpine shrubland and grassland communities, in addition to the mesic forest in Kaupo Gap. These are encouraging programs, and they clearly demonstrate that managing areas with intelligence and commitment is effective.

The integrity of the national parks in Hawai'i, as elsewhere, is increasingly dependent upon conditions beyond their borders. On Maui, TNC's Waikamoi Preserve shares a common boundary with HALE, and the fruitful exchange of help and advice, from an early stage before the Preserve was established, provides an example of how the NPS can positively affect adjacent areas. Similar interactions with major landowners, such as the

State of Hawai'i, will become increasingly important in the future.

STATE DEPARTMENT OF LAND AND NATURAL RESOURCES

The State of Hawai'i is the largest landowner in the Islands and holds over 2,360 km^2 in protected (P) subzones or Natural Area Reserves (NAR's). This represents 63% of all protected lands in the State. Controversy constantly swirls around these lands and focuses on 2 primary issues: do they encompass all the areas and ecosystems needing protection, and are they being managed properly.

Few would argue that the Hawai'i Department of Land and Natural Resources (DLNR) has not done a good job assembling its Seabird Sanctuary, which now includes 35 islands extending from Kure Atoll to Keaoi Island off the Ka'u coast. The State actively protects waterbird habitat throughout Hawai'i, but we are not concerned here with waterbirds. Instead, our interest is in the forests of the major islands, where conflicting issues arise on most State-owned land. Should logging, ranching, public hunting, or development be allowed? How does land management, or its lack, affect watershed value? How can access be provided to land locked by private ranches? Should huntable species be encouraged, further introduced, or eliminated entirely, and where should all this take place? Where will the money come from to undertake active management programs? What plant and animal management is desirable and practical?

Although DLNR is clearly aware of most of the concerns of the conservation community, it is not surprising that a prioritized listing of management actions for State-owned forests lands is desired by State officials. The conservation community, which includes a number of DLNR employees, has recently responded to this request (Stone and Stone 1984) with a list of 10 major issues (with peripheral lists developed by subsets of the participants) in a survey of concerned individuals in Hawai'i. While the lists contain many specific proposals, the number one priority, "identify and protect pristine and near pristine ecosystems", sounds much like a DLNR request for further information and may not be too helpful in its own right. Reasons why many of the listed actions will be politically difficult were given by R. Walker in an appendix to Stone and Stone (1984).

Where does conservation go from here on State lands? One recommendation would be to push for important programs, using the recommendations in Stone and Stone (1984). The development of reserves on Hawai'i's

Pu'uwa'awa'a Ranch (no. 2 priority) is well under way. FWS, with NPS help, is developing a program to control pigs within po'ouli (Melamprosops phaeosoma) range (no. 7 priority), which is a direct outgrowth of HALE's crater fencing program and the Hawai'i Forest Bird Survey (Scott et al., in press). The Sierra Club and Hawai'i Audubon Society are pursuing mouflon sheep (Ovis musimon) eradication on Mauna Kea (no. 5.5 priority). More action is sure to follow.

I would recommend that conservation groups use as much of their energy as possible working with, rather than against, DLNR. We all understand that confrontation does and will continue to occur. There are, however, vast problems about which DLNR personnel and other concerned individuals can sit down to focus creative, positive energy to bring about needed actions. It is possible to lobby for more financial support for DLNR at higher State levels, rather than rail against the agency for perceived failings. This will involve public education (no. 3 priority) at all levels in Hawai'i. Where important management actions may be impossible for DLNR to undertake because of a lack of manpower or funds, outside volunteers could be utilized to help. Although such cooperation may not always be possible, it should become an important part of the overall conservation strategy in Hawai'i.

CONSERVATION GROUPS

C.H. Lamoureux split the activities of conservation groups into 4 general categories, as follows:

1. The Eager Assistant.
2. The Watchdog.
3. The Gadfly.
4. The Legal Adversary.

The categories are sufficiently descriptive to need little elaboration, except to say that an "educator" function is more evident at levels 1 and 2. Although some individuals, and a few issues, fit neatly into one category or another, events tend to move them about, often (lamentably) toward confrontation. The major question posed is how to keep events at the Eager Assistant and Watchdog levels and still accomplish adequate preservation and management.

In essence, activity in the Eager Assistant level is alive and well, and this needs emphasizing. The Hawai'i Audubon Society continues to publish 'Elepaio, the major State conservation newsletter, lead hikes and outings, present slide talks, and provide input on many major conservation issues. The Sierra Club, numerous hiking clubs, botanical societies and garden clubs, environment centers, and museum and university staff are all actively providing information and support for the numerous agencies. A large and growing corps of volunteers is helping NPS, TNC, and FWS in their conservation programs. Employees from the major State and Federal land-managing agencies are included in the memberships of the largest conservation groups; indeed, to select only 2 of many examples, a DLNR biologist edits 'Elepaio and a NPS Superintendent serves on the executive committee of the Maui group of the Sierra Club. What we want to do is keep our activities at the "Eager Assistant" level whenever possible, while recognizing that an escalation to "Legal Adversary" may at times be unavoidable. When it happens, we must still strive to keep the personal interactions between opposing parties as positive and productive as possible. In general, this appears to happen. When legal recourse occurs, conservation groups also have other avenues available to them. They can work with elected members of State and county governments, and help educate the press. And their participation in symposia and surveys can continuously inform land managers and the public about Hawai'i's major environmental issues.

POLITICAL REPRESENTATIVES

A major message from the political arena was that local government needs accurate information from the conservation community upon which to base its decisions. We cannot expect our planning commissions, county councils, or State representatives to know what is best for the environment without our active input. In the world in which they move, they are continuously subjected to lobbying by vested interests whose perspectives are generally exploitative and self serving rather than protective and in the best interests of the Islands. Our elected representatives are accessible, and many of them will support conservation causes if they can be informed of them. They do like to hear our opinions, and there is a real opportunity for input that we often miss, simply because we don't make the effort. We are as often unaware of this opportunity as our legislators are unaware of the information that we wish they would act upon. Constant meaningful dialogue is the essential ingredient if we are to effectively enlist the support and aid of our elected representatives.

PRIVATE LANDOWNERS

The owners of large ranches on Hawai'i's Kona coast sent their concerns to the Symposium in the care of H. Peter L'Orange. Four major problems, as follows, have resulted in a deteriorating relationship between the large landowners and the scientific community. Individuals requesting access to private land:

1. Have not been honest about the true scope of their research.
2. Have not communicated their findings to the property owners prior to publication of data.
3. Have conducted research in areas other than those for which permission was given.
4. Have threatened possible government action if access was not granted.

It is not surprising that large landowners, facing such problems, deny further access to their lands, certainly for individuals known to act as noted.

The solutions to these concerns are obvious: Golden-rule behavior on the part of everyone working on private land, honesty of purpose, and communication of findings. The solutions clearly involve a respect for the landowners and their property. What is surprising is that such principles of respect have been violated often enough to cause palpable hard feelings; the majority of biologists working in Hawai'i regret this development and will honor the wishes of the landowners. Those causing the problems should do so also, no matter how much they disagree with land use practices or how self-righteous they feel.

However, the respect desired by the landowner is not always shown by him to the irreplaceable natural resources under his care. The needs of natural communities of organisms of national and international value should, insofar as is possible, be considered in overall stewardship of the land. As with political representatives, continual dialogue is necessary so that conservationists are aware of the problems of landowners and can alert them to current environmental concerns. It is unfortunately true that economic incentives are lacking in Hawai'i for managing the land for natural communities.

BIOLOGISTS

Biologists need to operate on 2 levels. First, they must continue to learn more about the components of Hawaiian ecosystems and how they interact. Second, they must convey this information both to their scientific colleagues and to the "outside" world. Information transfer must extend far beyond the classroom so that it reaches landowners, land managers, government officials, and the public at large through the news media. As indicated above, these groups need information upon which to base their actions. The problem is that the need for information acquisition and transfer exceeds the capacity and probably the capability of university and other biologists to meet. A further problem is the conflict between scientific objectivity and resource advocacy, which has often arisen in

Hawai'i, where numbers of trained and concerned individuals are limited and conflicts arise over natural resources that are deteriorating and scarce.

HAWAIIAN PEOPLE

The Office of Hawaiian Affairs traditionally concerns itself with the needs of members of the Hawaiian community as they relate to their lives, land, and culture. In attempting to define and shape that culture, they can offer much of value to all people in Hawai'i. Biologists also have a great deal to offer the Hawaiian people. Foremost is the gift of understanding Hawaiian natural history that so obviously fits into the context of much of the Hawaiian heritage. Conservationists can work hard to protect intact examples of the Hawai'i that shaped human development in the Islands. It is clear that the interests of conservationists merge with those of Hawaiian groups on these fronts.

Another area where a combined focus can help is the issue of watershed quality, so critical as a manifestation of 'aina (love of land) and for traditional Hawaiian agriculture. The important dimension is dialogue, as usual, which if maintained, could contribute to the enrichment of both Hawaiian culture and natural resource preservation.

GROUP INTERACTION IN BEHALF OF HAWAIIAN ECOSYSTEMS

There are many groups and people in Hawai'i who care deeply about the welfare of native Hawaiian plants and animals. This concern is an important resource. There will always be less than universal agreement among the various groups, but it is imperative that they work together to steadily preserve and improve the condition of that which remains, and to restore, as much as possible, that which has become degraded. No one agency, no single person, can begin to do it all. But by working together, conditions can improve. In the last few years there have been several programs that clearly point to improvements in the plant and animal habitat throughout the State, even though much has also been lost.

As an example, the results of the FWS Forest Bird Survey provided a database that attracted TNC to the Islands to launch their Endangered Forest Bird Project. TNC actively recruited biologists from FWS, NPS, DLNR, the University of Hawai'i, and the Bishop Museum to help prioritize important natural ecosystems that needed protection. Waikamoi Preserve on Maui and Kamakou Preserve on Moloka'i were acquired within 3 years, and preserve managers are actively attempting now to control introduced plants and animals in these areas. On Maui, where TNC and NPS now share a common boundary, joint management programs are demonstrating how cooperative efforts can effectively manage problems that transcend legal boundaries.

If we are to continue to preserve and manage our native ecosystems, we must look forward with optimism and build on our successes. We should recall that the NAR's, the FWS system of waterbird refuges, and TNC's forest bird program all had their genesis very recently. The national parks have essentially solved their feral goat problems in HAVO and are well on their way to doing the same at HALE. They have recently made giant strides in their feral pig control program. DLNR eradicated most of the feral sheep and goats on Mauna Kea, indicating the power of conservation organizations and courts, and the willingness and ability of the State to comply. The results of the cooperatively run FWS Forest Bird Survey have allowed us to prioritize important forest areas and have helped lead to the development of preserve designs and the acquisition of forest bird habitat. The Endangered Species Act of 1973 has made it more difficult to ravage important areas. New know-how continues to improve our management options and motivate us to act. Conservation awareness is extending further into business and policy-making communities. Even though the magnitude of our losses in Hawai'i over the last 15 centuries has been enormous, we are now moving to correct many past abuses to the land and protect many remaining gems. The growth of integrated and well-planned conservation programs within the past 15 years shows that we can make a difference.

LITERATURE CITED

Scott, J.M., S. Mountainspring, F.L. Ramsey, and C.B. Kepler. In press. Forest bird communities of the Hawaiian Islands: their dynamics, ecology, and conservation. Stud. Avian Biol.

Stone, C.P., and D.B. Stone. 1984. The "10 most-wanted" management actions for terrestrial Hawaiian ecosystems: a survey. Elepaio 45:41-48.

Walker, R.W., J. Medeiros, R.E. Saito, T. Telfer, D.H. Woodside, S. Swedberg, P. Sekora, and C.F. Zeillemaker. 1977. Hawaii waterbirds recovery plan. Portland, Ore.: U.S. Fish Wildl. Serv.

V. CONCLUSION

19.

HAWAI'I'S NATIVE ECOSYSTEMS: IMPORTANCE, CONFLICTS, AND SUGGESTIONS FOR THE FUTURE

Charles P. Stone and J. Michael Scott

The convening of this Symposium was neither the beginning nor the end of the vital process of cooperation and meaningful communication on behalf of Hawai'i's native ecosystems. Our objectives were to provide in one place a current overview of the subject, to involve a variety of responsible agencies, organizations, and interested users in discussing the problems, and to improve the chances for better understandings and management of Hawai'i's lands in the future. Because the first two objectives have been met we think that there is increased hope for the third. The purpose of this chapter is to try to increase the appreciation of the importance of native Hawaiian ecosystems to all of us, to candidly outline some general conflicts and motivations of key groups, and to provide some suggestions for working together.

REASONS FOR PRESERVING NATIVE ECOSYSTEMS

The authors of the foregoing papers provided us with compilations of what is known and offered suggestions as to what we need to know and do to protect Hawai'i's native ecosystems. They also touched on biological reasons for preservation and management of these unique areas. There are a number of reasons, both biological and non-biological, for preserving Hawai'i's remaining native ecosystems. They include:

1. Aesthetic and recreational values.
2. Hawaiian cultural uses.
3. The need to preserve genetic diversity for utilitarian purposes.
4. The need to preserve natural processes and gene pools.
5. The need for environmental baselines, for research and education areas, and for improving land-use decisions.
6. Watershed and climatic values.

7. Ethical considerations.

8. Constitutional, statutory, and planning mandates.

Aesthetic and Recreational Values

Tourism is the State of Hawai'i's number one industry, accounting for $323 million in tax revenues in 1980, about 8 percent of the population at any one time, and bringing about $3 billion per year into the State (Morgan 1983). Tourism can directly influence Hawai'i's population growth patterns now and in the future (Bank of Hawaii 1984). Although the industry is dependent on the general state of the economy, leisure time, and technology (especially on the U.S. Mainland and in Japan), people visit Hawai'i for a number of specific reasons. Among these are the quality of the environment, including the clean air, oceans, beaches, and forests, and the scenic vistas. A general concept of "escape" is also important (Bank of Hawaii 1984).

Negative effects of concentrated tourism on residents (as opposed to nonresident investors and visitors) have been suggested, including increased crime, low per capita income, and an undiversified and precarious economy (Stannard 1985). State policies since the 1960's have involved "redistributing growth to the neighbor islands," partly as a result of problems such as urban sprawl on O'ahu (Chow 1983), and also because of regional economic and development needs. Environmental problems related to tourism and population growth are outlined in the background material to the Hawai'i State Plan (Hawai'i Department of Planning and Economic Development 1978).

If Hawai'i becomes "just like other places, with the same traffic jams and fast-food restaurants as elsewhere," uniqueness and escape qualities will be lost (Morgan 1983; Bank of Hawaii 1984). According to the Bank of Hawaii (1984), keeping Hawai'i from future decline as a visitor destination "will probably involve the difficult move back away from mass marketing that has so characterized it in recent years." Selective promotion may provide an answer to anticipated future tourist (and especially new visitor) decline leading to economic instability.

Part of Hawai'i's distinctiveness that is becoming increasingly valued rests in the unique native ecosystems that still remain. Improved understandings (education) about these areas can result in increased enjoyment for Hawai'i's visitors and residents; there is also the additional benefit of attracting more educated, discriminating, and well-to-do users to less crowded areas. Native ecosystems and the uncrowded ambience and aesthetics they project could be increasingly important and unique attractions to photographers, backpackers, hikers, campers, birdwatchers, hunters, etc. from overseas and Hawai'i. Specific planning for the future of these areas is badly needed.

Hawaiian Cultural Uses

The effects of ancient Hawaiians on the land and the reciprocal effects of the land on the people have been well documented (Degener 1930; Malo 1951; Handy and Handy 1972; Kamakau 1976). Many utilitarian plants and animals which affected native species were brought with early voyagers from ancestral homelands, and the new Hawaiian landscape was much modified to suit the [immediate] needs of the people (Kirch 1982). Zimmerman (1963) went so far as to state that Polynesian man "treated most of the forest as an enemy" and it is known that extinction rates of animals prior to arrival of European man in Hawai'i were high (Olson and James 1982; Gagne and Christensen, this volume). Yet native ecosystems and their products were--and are--important in Hawaiian culture (Degener 1930; Malo 1951; Handy and Handy 1972; Kamakau 1976). The system of Hawaiian land divisions and zones which includes native as well as modified ecosystems (Malo 1951; Handy and Handy 1972; Kamakau 1976) suggests that the Hawaiians visited and used most of these areas, including the subalpine, where shrines, shelters, and adze quarries have been found.

The Office of Hawaiian Affairs (OHA) Cultural Plan "seeks to maximize the traditional Hawaiian use of land and natural resources in conjunction with human and cultural systems, for religious, recreational and economic purposes" (Office of Hawaiian Affairs 1984). Spoehr (1984) believed that major aspects of resource management in Hawaiian culture included reverence for life, appreciation for intrinsic natural values, a concept of stewardship, and a sense of place. All of these were closely interrelated. As a part of traditional Hawaiian culture, OHA stresses ties to the land, including resource inventory, land acquisition and dedication, and preserving and managing the land to assure "traditional uses." The ahupua'a traditional land unit (generally a mountain-sea economic/cultural unit) is certainly amenable to ecological and watershed management as well.

Tangible native Hawaiian interest in native ecosystems is manifested by OHA's consideration of a proposal from The Nature Conservancy to protect native forest from feral pigs on Moloka'i; a natural resource inventory initiated by the Office of Hawaiian Home Lands (H. Spoehr, pers. comm.); and a resolution to preserve Hawai'i's native forest, prepared by OHA (Appendix 1).

The Need to Preserve Genetic Diversity

Native Hawaiian ecosystems may be viewed as vast storehouses of information available in genes that can be used by future generations for meeting continuing medicinal and agricultural needs. The richest of such depots, with 40-50% of the planet's species (Myers 1980), are tropical rain forests, currently disappearing more rapidly than other ecosystems on a world-wide basis. (Every minute, over 12 hectares (30 acres) are lost, and by the year 2,000 only degraded patches of forest will be left (Caufield 1985)). Loss has been estimated at 10-20 million hectares per year (1-2% of the forest) (U.S. Department of State 1980), or an area the size of California (Caufield 1985). In Hawai'i, in addition to rain forests, lowland mesic and dry forests, where plant diversity is high, and high elevation koa (Acacia koa) forests are very scarce (Jacobi and Scott, this volume).

Oldfield (1984) called gene resource conservation a "socioeconomic necessity" and believed that these resources and their habitats might be our "most important economic and political assets." Balandrin et al. (1985) summarized some of the uses made of native plants in industry and medicine:

> Many higher plants produce economically important organic compounds such as oils, resins, tannins, natural rubber, gums, waxes, dyes, flavors and fragrances, pharmaceuticals, and pesticides. However, most species of higher plants have never been described, much less surveyed for chemical or biologically active constituents, and new sources of commercially valuable materials remain to be discovered. Advances in biotechnology, particularly methods for culturing plant cells and tissues, should provide new means for the commercial processing of even rare plants and the chemicals they produce. These new technologies will extend and enhance the usefulness of plants as renewable resources of valuable chemicals.

Natural rubber, palm oil, jojoba (Simmondsia chinensis), numerous wood products, a drug effective against leukemia, and 40% of all prescriptions written in the U.S. are derived from plants, many from tropical areas. Over 70% of plants with anti-cancerous properties are from rain forests (Myers 1984), and several drugs in use for this purpose are also derived from animals (Oldfield 1984). Artificial selection of native tropical plants holds promise for alleviating hunger and improving agricultural productivity. A perennial corn has been discovered in southern Mexico forests (Stoel 1980), and a sticky, insect-resistant potato has been found in Peru (Oldfield 1984). The wild forest-dwelling progenitors of other food crops maintain a source of genetic diversity available when needed to improve highly selected agricultural strains vulnerable to disease and insects. In Hawai'i, one of the few places in the United States with rain forest, unique forms are still being discovered, genetic diversity is high, and potential plant uses for agriculture and medicine are largely unevaluated. A screening program for anti-leukemia drugs in Hawaiian plants has been sponsored by the National Institutes of Health (C.W. Smith, pers. comm.).

The Need to Preserve Natural Processes and Gene Pools

Knowledge about functional processes (in contrast to structural composition) of native ecosystems, involves understanding complicated interrelationships. Examples are: the cycling of nutrients, water, etc.; successional changes in communities over time; responses to stresses such as human intervention; responses to natural environmental perturbations such as storms and climatic cycles; effects of native ecosystems on weather patterns; population dynamics of plants and animals; speciation through gene pool disorganization and reorganization; and evolution in general under near-natural conditions. The man-induced changes that have already influenced many of these processes (Schonewald-Cox, this volume) in most places make the need to preserve more of the unaffected places more immediate.

Knowledge about natural processes is "essential for management purposes because it integrates ... environmental relationships and allows prediction [our emphasis] of the effects of one part of the system on the others" (U.S. Department of State 1980). If mankind is to effectively modify his environment with minimal long-term damage and maximum advantage to himself, there is a need to fully understand what is changing. Knowledge of existing natural processes that have proven effective and durable is vital in this regard.

Hawaiian ecosystems have developed in "splendid isolation" and contain perhaps the best examples anywhere of adaptive radiation and other evolutionary processes. Gene pools of forms which have undergone severe selection as a result of colonization over extreme distances; which have developed in a disharmonic biota without many of the biotic hazards elsewhere; and which have filled extremely varied niches in the Islands with small populations, are worthy of preservation because they are especially unique in the world.

The Need for Environmental Baselines, for Research and Education Areas, and for Improving Land-Use Decisions

Protected native ecosystems and natural areas can offer many benefits to Hawai'i's citizens interested primarily in other land uses, including development. Protected (undeveloped) areas can provide baseline information on environmental quality (air, water, and land) to better assess desirable and undesirable aspects of different kinds of development and consumptive uses elsewhere. Managers of natural areas can work cooperatively with developers as orderly development occurs, so that adversary situations costly to all can be prevented. Native ecosystems provide comparison sites for applied and basic research and can be used to help encourage development suited to ecological, socioeconomic, and traditional uses of local communities.

In attracting, maintaining, and coordinating a cadre of scientists and educators of various disciplines, protected areas can provide a focus for present and future problem solving in Hawai'i and the world. Kepler and Scott (in press), and Loope and Stone (1983) have suggested that international as well as local and regional focus on scarce island ecosystems and alien organisms is desirable to increase efficiency in problem solving. Some of this can be accomplished through enhanced communication about research and management on protected areas. Protected areas can also help focus cooperation among conservation and development constituencies in local and regional land use planning, increasing understandings and reducing conflicts and costs. In summary, protected natural areas can provide an umbrella under which "people solve problems at the local, regional, and global levels" (Gregg 1984).

Watershed and Climatic Values

Removal of forest cover in many areas of the world has resulted in altered climatic regimes and reduced watershed values (Myers 1984; Forsyth and Miyata 1984). Hawai'i is no exception. Dry seasons may be extended and intensified (Weisburd and Raloff 1985) and flooding may increase because of lack of vegetation. Forests retain and cycle moisture and may generate considerable rainfall locally. According to the U.S. Department of State (1980),

> deforestation may affect clouds by increasing the level of atmospheric carbon dioxide or by increasing the amount of sunlight affecting the earth. The resulting climatic changes could have catastrophic impacts upon agriculture.

Continued tropical forest losses may contribute to destabilization of the earth's climate in the 21st century (U.S. Department of State 1980).

Rain forest soils are often low in nutrients because the luxuriant growth present before rain forest removal concentrates most of the available nutrients. They are thus unsuitable for long-term agriculture after forest clearing and generally become barren scrub forest when abandoned. Further, the complexity of the vegetation, its age, effects on ambient environment, and, in the case of Hawai'i, the presence of alien plant propagules that out-compete natives on disturbed sites, make wet forests especially, and many other forest types as well, truly irreplaceable (Gomez-Pompa, Vazquez-Yones, and Guevera 1972). Alien tree plantings (often monocultures with little diversity) cannot duplicate the positive watershed and climatic values of complex native Hawaiian forests, much less other values. Some alien plantings increase runoff because they "waterproof" topsoil. Reduced understory (often weedy aliens) and ground cover under regularly spaced, even-aged plantings of introduced species often allow rapid runoff. Continued removal of trees for forest products further depletes scarce nutrient supplies.

Forest Reserves in Hawai'i were established and protected primarily for watershed values. Early sugar planters and foresters realized that "a forest cover most effectively promoted the infiltration of rain water that nourished springs and ground water" (Street 1983; see also Judd 1927). Forest Reserves were set up, feral stock was controlled, and planting programs were initiated. The increasing demand for more water for urban, agricultural, industrial, and other uses emphasizes the continuing need for native forests. According to Peterson (1983), "loss of land through erosion, siltation of inshore waters, and flood damage are serious problems in Hawaii." Significant problems related to Hawai'i's watersheds are identified in the background material for the Hawaii State Plan (Hawai'i Department of Planning and Economic Development 1978) for each island. Removal of forests in Hawai'i has slowed in the past decade, but little is left and deterioration is continuous and widespread.

Ethical Considerations

It can be argued that man bears some responsibility as a rational being for living things beyond himself, even if their utility is not readily apparent. The potential for destruction of other life forms by man is enormous and often occurs inadvertently. Yet the intricacy, order, and wonder of what has developed over the millenia should be valued more highly by the advanced forms we pretend to be. Surely part of our concern for rare species and ecosystems is the simple realization that once they are gone, we have somehow failed in our responsibility for other life dependent upon us for existence.

Constitutional, Statutory, and Planning Mandates

Among the most important documents addressing Hawai'i's native ecosystems are the Constitution of the State of Hawai'i, the Hawai'i State Plan, various County Plans, the Hawai'i Revised Statutes, the Hawai'i Wildlife Plan, Hawai'i's Renewable Resources Research Plan for the 80's, the Federal Endangered Species Act of 1973 and various recovery plans, and the Department of Land and Natural Resources Regulation No. 4. These documents provide considerable authority and direction for active, effective, and vital programs. It is probably fair to say that problems arise in interpretation and implementation of directives rather than in authority or written good intentions. Indeed, the gap between the written rhetoric and the necessary people, dollars, bureaucratic freedom, coordination, understanding, and initiative to accomplish what is needed seems particularly large in Hawai'i. Hawai'i's small size, insularity, attractiveness to people, isolation, endemism, and fragility compound problems found elsewhere. A brief look at some of the enabling language related to native ecosystem protection and management follows, and more extended references are provided in Appendix 2.

Constitution of the State of Hawai'i, Hawai'i State Plan, and County General Plans. In general language, the Constitution gives the State the power to maintain a healthful environment, prevent excessive resource demands, and protect and enhance natural resources. The Hawai'i State Plan (Hawai'i Department of Planning and Economic Development 1978) provides a general guide to implementing development and conservation statewide, and an overall goal is to achieve a "desired physical environment characterized by beauty, cleanliness, quiet, stable natural systems [our emphasis] and uniqueness, that enhances the mental and physical well-being of the people."

Like the Hawai'i State Plan, County General Plans are long-range guides to growth and development but are usually limited to one island. The Hawai'i County General Plan (County of Hawai'i Planning Department 1971), as an example, identifies the following areas as worthy of consideration for "protection and conservation of natural resources": areas necessary for specified endangered wildlife and for conservation of natural ecosystems of endemic plants, fish and wildlife [our emphasis]; lands necessary for preservation of forests, park lands, wilderness and beach areas; lands with a general slope of 20% or more or that are unusually scenic; lands necessary for watershed, water source or water supply protection; and lands not normally adaptable or needed for urban, rural, agricultural, or public use.

Hawai'i Revised Statutes (HRS). The Statutes provide considerable authority for the Department of Land and Natural Resources (DLNR) to manage and administer State lands and their resources. Included are regulations governing importation of plants and animals, establishment of natural areas [our emphasis], the authority to conduct inventories and research, and the authority to enter into agreements with Federal agencies and counties on behalf of native species and ecosystems [our emphasis]. An Animal Species Advisory Commission, an Aquatic Life and Wildlife Advisory Committee for each county, and a Natural Area Reserve Commission are to inform and coordinate with DLNR or the Board of Land and Natural Resources (BLNR).

Hawai'i Wildlife Plan. The Hawai'i Wildlife Plan is "intended to provide an integrated strategy towards solving the most critical wildlife problems." The goal is to give direction to the State's wildlife program in order to: perpetuate and increase game, non-game and threatened and endangered wildlife species for their intrinsic, recreational, scientific, educational, or food source values; prevent adverse impacts of wild animals on man and his operations or native ecosystems [our emphasis]; and improve qualitatively and quantitatively the public's use and enjoyment of the wildlife resources (Hawai'i Division of Forestry and Wildlife 1984).

The Plan assumes that: 1) the State population will continue to increase, as will (at least proportional) demands on wildlife and habitats, 2) wildlife habitats will continue to be influenced by land use changes, pollution, and "exotic sources", 3) wildlife will continue to be adversely affected by environmental contamination and degradation, disease, etc., and 4) the State will continue to recognize its "obligation to the wildlife resources, particularly those that are endangered", and "will support a program of protection, conservation, research, management, and improvement" [our emphasis].

Hawai'i's Renewable Resources Research Plan for the 80's. This plan defines a forest conservation research program for Hawai'i during the 1980's. It is the result of cooperation among State, private, and Federal interests and is the third such effort. The Plan identifies staffing needs in 11 research and management areas, including "native ecosystems." In the

80's, 403 scientist years have been identified to address "ultracritical" native ecosystem problems. Included are characterization of habitat requirements, life history studies, and management recommendations for rare native plants and animals. The Plan provides a yardstick with which managers and researchers can measure long-term progress.

Endangered Species Recovery Plans. The Endangered Species Act of 1973 and its subsequent amendments direct all Federal agencies to protect and restore Federally listed endangered and threatened species and their habitats (U.S. Congress 1973); states are encouraged to manage resident endangered species. "Recovery Teams" consist chiefly of professionals from different agencies with responsibilities for the species of concern; their primary objective is to produce "Recovery Plans" which will result in removal of species from "Endangered" or "Threatened" status by making them self-sustaining members of ecosystems (Porter and Marshall 1976). The Director of the U.S. Fish and Wildlife Service (FWS) approves team members. Plans are reviewed, approved, and circulated by a Regional Director of FWS. Tasks are assigned to different agencies with the understanding that funding to accomplish goals may or may not become available. In Hawai'i, the U.S. Fish and Wildlife Service often uses consultants to prepare recovery plans, and teams are not generally involved in implementation of plans.

Recovery plans include those for endangered Hawai'i, Kaua'i, and Maui-Moloka'i forest birds; for the Hawaiian goose (Nesochen sandvicensis), 'alala (Corvus hawaiiensis), 'io (Buteo solitarius), and palila (Loxioides bailleui); for Hawai'i waterbirds and Northwestern Hawaiian Islands passerines; for the Laysan duck (Anas laysanensis) and Hawaiian seabirds; and for the Hawaiian wild broad bean (Vicia menziesii).

Recommendations for what the recovery team considers "Critical Habitat" as defined under Section 7 of the Act (designated via publication in the Federal Register and a review process) are made in recovery plans, and recommendations for acquisition of private lands are included in some cases. Recently the term "essential habitat" has been used to avoid the legal process, especially in Hawai'i (Juvik and Juvik 1984). A Composite Recovery Plan, which provides a synopsis of all approved plans, is being prepared by the U.S. Fish and Wildlife Service to condense information and facilitate understanding (P. Stine, pers. comm.).

Recommendations for habitat acquisition and the unlawful actions designated under Section 9 (Prohibited Acts) make this Federal legislation important to private and State landowners in Hawai'i, and have resulted in some of the conflicts mentioned in the Session IV summary of this Symposium. However, the Act "imposes no authorities or obligation on the actions of private agencies, individuals, or corporations" (unless Federal funding is involved), with regard to land use (Wydoski 1977; Cooper 1979). Ethical considerations, lack of knowledge, scientific and bureaucratic inertia, emotional reactions for and against preserving endangered species, and economic motives are probably also important in causing conflicts related to the Act in Hawai'i.

DLNR Regulation No. 4. Hawai'i passed the first land use law of all the States in 1961, which established a State Land Use Commission (LUC). This Commission was charged with classifying and regulating use of all lands with the main purposes of encouraging "orderly and efficient development of land for urban use...", protecting agricultural lands, and providing "maximum economy and efficiency in public services and utilities" (Armstrong 1973). The Law is administered by the State Departments of Planning and Economic Development, DLNR, and Taxation; the Counties of Hawai'i, Kaua'i, and Maui; the City and County of Honolulu; and the University of Hawai'i. Four districts provided for in the law in 1963 and 1965 amendments were Urban, Agricultural, Conservation, and Rural. The Conservation District includes national and state parks, lands with a slope of 20% or more, lands in existing forestry and water reserves, and marine waters and offshore islands. The DLNR administers the Conservation District, and District boundaries can be changed by the LUC through petition and public hearing.

DLNR Regulation No. 4, which became effective in 1978, provides for land use within the Conservation District, including subzones, uses, appeals, enforcement, and penalties (Department of Land and Natural Resources 1978).

Regulation 4 established a Protective "P" Subzone to "protect valuable resources in such designated areas as restricted watersheds, fish, plant, and wildlife sanctuaries, significant historic, archaeological, geological and volcanological features and sites, and other designated unique areas." The "P" Subzone includes 236,345 ha (Holt and Fox, this volume), nearly 57% of all Hawaiian natural areas. Permitted uses do not allow physical facilities (except government development where public benefit outweighs impact), but do allow habitat improvement, site restoration, vegetation protection (including noxious plant removal), and control of animals and plants including fishing and hunting. Other subzones and regulations are outlined in Appendix 2.

A great deal of authority is vested in the Board to change boundaries and classifications and permit variances within the Conservation District. In Hawai'i, where unemployment is high and good jobs scarce in some areas; where the economy needs to be diversified for stability; and where the emphasis on self-sufficiency from remote markets (including food and energy production) is great, the pressures on Conservation District lands are increasing. When a commercial interest for the land is found, there is often a desire to change the status of the land. Because the State inventory contains many important native ecosystems (Holt and Fox, this volume), there is considerable focus on these lands and their stewardship.

CONFLICTS WITH OTHER LAND USES

Private Lands

There are two major kinds of conflicts between those primarily interested in preserving and managing native ecosystems in Hawai'i and those evidencing more interest in other values. First, there is disagreement about the future of native ecosystems on private lands. A common scenario involves a private landowner or conglomerate with deep roots in Hawai'i; a sometimes paternalistic attitude about what is good for Hawai'i's people (immediate jobs, development, etc.); with considerable acreage under control and some political influence; and with a (justifiable) profit motive and strong beliefs in private enterprise and property. In the opposite corner are a small number (often not a group) of individuals who value native ecosystems because they understand something about their (often non-economic) importance and rapid disappearance; who strongly believe that some developments are incompatible with the maintenance of those ecosystems; who often take time to write articles in newspapers and other outlets to inform others; who join environmental groups to preserve what they value; and who sometimes are willing to enter litigation on behalf of preservation.

Some landowners feel that the environmental "opposition" has betrayed landowner efforts to cooperate in the past, through abusing access and other privileges (Kepler, this volume). They argue that researchers and educators have studied and documented endangered species abundance or recommended that plants or animals be listed without discussing objectives or findings with landowners who provided access. They find their land use practices criticized, photographed, and published without further discussion or serious attempts at understanding. They point to trespassing on private property without permission--all in the name of conservation.

Many landowners seem to believe that researchers and educators should stick to professional functions, and that credibility is lost when they become advocates for conservation (H.P. L'Orange at this Symposium). Others believe that their own livelihood and rights are being challenged, perhaps by a small number of people with different values and lifestyles, and by bureaucracies and legalities that do not display an understanding of economics or other facts of life. Making an adequate living in marginal economic circumstances seems far more important than many of the demands and wishes of others who do not own and work the land. Many private landowners consider themselves good conservationists and insist that they value and care for the lands under their control so that they can continue to make a living from them. Some are uncertain about what makes one area more unique or valuable ecologically than another, and about how many areas need to be preserved.

Many of those who are primarily interested in preserving native ecosystems free of other uses may dogmatically insist that koa cannot be harvested, 'ohi'a (Metrosideros polymorpha) cannot be clearcut and chipped, hapu'u (Cibotium spp.) cannot be taken for export, and feral animals including cattle (Bos taurus) cannot be allowed, if native ecosystems are to remain viable. Many are disturbed at what they perceive to be lack of understanding by the landowner and emphasis on the immediate profit motive rather than what they believe is a more important obligation for the future. Some resent the denial of access to private lands, which keeps them from understanding important ecosystems before they disappear. They suspect the landowner of hiding something.

Many native ecosystem advocates do not trust the objectivity of the private landowner to practice conservation in the face of economic necessity. They point to apparent disregard of State and Federal laws, regulations, and agreements on private lands in Hawai'i (e.g. Newman 1984a, b; Clark 1985; Lockwood 1985). Some proponents of preserving native ecosystems are concerned about apparent half-truths or misleading statements from private landowners about forest management and conservation. They are disturbed about emphases on "decadent" forests, "maintenance" forestry and "enrichment plantings" (Yates 1984; Mueller-Dombois, this volume) to increase forest "vigor", and the apparent lack of understanding about old growth stands and natural processes such as dieback. The difficulty of regenerating what nature has produced (Lamoureux, this volume) seems unappreciated.

Public Lands

A second source of conflict about Hawai'i's native ecosystems involves public (mostly State) lands. Here, those who are primarily interested in preservation and management have many of the same concerns mentioned above for private lands. Most public land managers have no direct profit motive; however, many who would preserve native ecosystems express distrust of the administering bureaucracies, which sometimes seem to act ultimately for political, economic, or self-serving reasons rather than conservation values. There is often a feeling that case-by-case decisions about native ecosystems are predetermined in favor of development; that without considerable outcry, "P" Subzone lands would be reclassified as profitable uses for them appear; that more variances would be granted, and more prohibited uses would be allowed with time; and that inertia, unresponsiveness, and lack of concern sometimes seem to predominate in State and Federal agencies.

State and Federal agencies are sometimes seen as excessively bureaucratic, with uninspired and inefficient leadership (even though some employees are recognized as dedicated and effective public servants working under severe constraints). Agency and political leaders are often viewed as having superficial or incorrect knowledge of what is vital ("ecosystem values"), and expending personnel and dollars on less important matters (facilities, hunting programs, administration, public parks, law enforcement, etc.). There is a certain amount of skepticism that administrators do not know what preservation priorities are most important, even though appropriate general statements and policies exist.

Those responsible for public (State and Federal) lands could argue that they are concerned about native ecosystems as well as other values, but that many users also value hunting and other forms of recreation over preservation of natural, undisturbed areas. Visitors to public areas must be protected and facilities must be safe. Limited dollars must be expended for these and other reasons as well as for native ecosystem preservation and management. The decisions must be based on all known values in each case, and sometimes preservation and management of native ecosystems will not be primary. Lack of support, lack of expertise, and conflicting mandates are also important factors in determining priorities (see Appendix by Walker in Stone and Stone 1984) for State and Federal agencies. Ultimately, the people and their representatives control much of this in a democracy. If people and politicians are not concerned, agencies cannot adequately fulfill responsibilities.

Politicians and those serving on the BLNR could argue similarly, with the added reminder that orderly economic development is behind much of the enabling language in State and County documents, and that many of Hawai'i's citizens need jobs. Also, there has been strong political emphasis on self-sufficiency in Hawai'i for energy production. Some would argue that opposition to geothermal development, for example, seems to have varying elements of the NIMBY ("Great idea, but ... Not In My Back Yard!") motive to it, rather than real ecological concern. Again, they might argue that decisions have to be made on all values in each case, and sometimes changing a permitted use or loss of a native ecosystem in order to obtain (perceived) greater self-sufficiency or economic viability is necessary. Public officials have also argued that scientists haven't made a clear case for what needs protecting, haven't provided answers to difficult natural resource problems, and that scientists/conservationists want to "save it all."

SUGGESTIONS FOR THE FUTURE

While many great truths and lofty principles are undoubtedly involved on all sides of the land use conflicts in Hawai'i, it seems to us that there is also considerable common ignorance, inertia, delusion, and self interest, covered by an increasingly thick veneer of decreasing possibilities. What is worse, there is an incredible waste of time and effort in conflict situations and enormous lack of knowledge about what is happening on the part of most citizens and visitors. Although nobody has all the answers, we think that there are a number of points that must be better addressed in future land use decisions in Hawai'i.

1. Some land uses are incompatible and decisions need to be made as to how to deal with this. Multiple use of some areas sometimes becomes multiple abuse (Juvik and Juvik 1984). One cannot have pristine old growth forest necessary to preserve some native birds, invertebrates, and plants, and harvest most of the koa or hapu'u or 'ohi'a in it, as has been proposed (see Holden 1985 for an excellent analysis of the 'ohi'a wood-chipping controversy). Nor can one easily regenerate native forest under current conditions. Subsistence or other use of alien animals or plants in native forests by some of Hawai'i's ethnic groups is not compatible with good native forest management.

We need to decide what areas statewide we can afford to preserve as intact ecosystems, acquire them if needed, absolutely prohibit conflicting uses and abuses in the future, and manage toward that end. The Federal government, The Nature Conservancy, and various nations have done this with some success, and the State of Hawai'i could also implement active compartmentalized land usage on their Natural Area Reserves (NAR's) and other lands, through fencing and other practices. The State has "set aside" 32,850 ha (81,000 acres) in the NAR system (Anonymous 1985) and owns much additional land in Conservation subzones and wildlife and plant sanctuaries (Holt and Fox, this volume), but protection and management beyond the paper designation are rare (Yates 1984; Holt and Fox, this volume). Support for the enduring, difficult, and expensive job of managing lands "set aside" for conservation is needed.

2. Case-by-case land use decisions should be minimized. Regional land use planning, including native ecosystems, is needed. One purpose of the early land use legislation and regulations was to reduce future conflicts. However, the system was established primarily to promote orderly economic development, and it is cumbersome (Chow 1983). It needs to be revised to incorporate more current ecological and developmental information and values (such as the U.S. Fish and Wildlife Service Hawai'i Forest Bird Survey data, and recent geothermal resource knowledge (Lawrence Berkeley Laboratory, California 1981; U.S. Department of Energy 1982a, b). Agreed-upon and manageable areas representative of our best native ecosystems need to be better identified (Stone and Stone 1984; Holt and Fox; Lamoureux; Schonewald-Cox; Franklin; Jacobi and Scott; Scott, Kepler, and Sincock, this volume). The Nature Conservancy's Heritage Program is currently synthesizing native ecosystem classification systems in Hawai'i developed by Gagne, Jacobi, Lamoureux, Mueller-Dombois, Smith, and others into what should be a practical system for land managers (R.A. Holt, pers. comm.). More involvement by user groups in developing the system will be needed at some point to ensure wide usage. Once such a practical system is accepted by most users, we may be able to better agree on priority areas and communicate our choices more clearly to decision makers.

An overall understanding of the place of native ecosystems in Hawai'i's future is badly needed by political, legislative, and agency leaders; the business community; private citizens; and scientists and conservationists. Decisions about conflicts between native ecosystems and other uses as they arise are not only costly and time consuming; they also preclude understanding of the overall picture, are made too rapidly, and can result in continual fragmentation and unplanned loss of our remaining native ecosystems. Better regional and statewide land use planning, and involvement of more knowledgeable individuals with varying expertise (including ecology) is needed. We have enough information now to begin to improve regional and statewide land use planning and implement better land use management for all purposes, if we can increase cooperative efforts toward that goal. Broadening of the practical land use planning base and an effective implementation strategy are needed. Decisions about leadership and practical mechanisms could be made in future forums, most appropriately under State leadership. The subject of effective interagency interactions for regional land use planning in Hawai'i could be a key topic for discussion.

3. <u>Private landowners should be rewarded</u> for caring for native ecosystems. As the situation now stands in Hawai'i, it makes more sense economically for a landowner to clear or develop land for immediate gain than to attempt to preserve and manage native forests for future generations. Although logical in the past, Hawai'i can no longer afford to perpetuate tax structures that encourage this. Nor can taxpayers ignore the realities of subsidizing poor resource and watershed management and encouraging climatic effects that will be to their detriment in the long run. Tax write-offs or other better means of providing economic incentives to landowners who value long-term conservation of native systems should be developed. A forum on this topic might be worthwhile. Private landowners should be publicly recognized by conservation groups and others for their conservation efforts; The Nature Conservancy of Hawai'i does this at present.

4. <u>The Department of Land and Natural Resources should be given adequate support</u> by the Legislature. The State of Hawai'i controls nearly 66 percent of Hawai'i's natural areas (Holt and Fox, this volume). The insufficient funding and inadequate staffing (Department of Land and Natural Resources 1985) of the primary State agency responsible for the wealth and uniqueness of Hawai'i's biota is regrettable. It is very unfortunate when a State conservation department today lacks both research and interpretive capability, does not have a trained ecologist, lacks sufficient support to deal adequately with the nongame programs emphasized in so many other states with less unique resources, and does not have enough support to actively manage the small Natural Area Reserve system under its stewardship. Although DLNR has to balance many mandates and accomplish the impossible (see Appendix by Walker in Stone and Stone 1984), it could do a far better job if there were more expertise, more

delegation of authority, and someone to delegate to. Use of outside consultants is an effective way to answer questions and should usually be cost-effective when in-house expertise is lacking.

5. Federal agencies need to improve interaction, understanding, and responsiveness. Federal agency personnel in Hawai'i are isolated from Regional Offices to which they are responsible, require orientation time to Hawai'i if they arrive from Mainland duty stations, often leave the Islands after a short tour of duty, need to respond to Mainland priorities to varying degrees, and often do not interact enough with local resource personnel for one reason or another. Backgrounds, training, and motivations differ, and communication is sometimes difficult, at least at first. Mistakes by Federal agencies have been and will continue to be made (Kepler and Scott, in press; Sun 1985). Yet Federal agency personnel need to respond in the context of Hawai'i's natural resource and economic needs and work within Hawai'i's social framework as well as for Mainland or agency priorities. The latitude to make individual judgements and to go beyond provincial agency interests, boundaries, and bureaucratic procedures is an important ingredient for achievement in Hawai'i.

Objectives of Federal, State, and local conservation groups are becoming more in tune, but there is still considerable polarization, and many opportunities for cooperative accomplishment are missed. Federal employees, who are often the "new kids on the block," should make extra efforts to understand, help, and learn from those who have deeper roots. At the same time, fresh ideas, technology, support, and leadership from Federal agency personnel are needed in conservation of Federal and other native ecosystems in Hawai'i.

Especially important is completion of work through the reporting stage prior to undertaking new projects or departure from the State, and the open review and distribution of plans and reports produced. Bureaucratic procedures and controls in both public and private sectors have greatly increased in the past decade and often seem designed to frustrate cooperation; but if Federal (and State) agency personnel take the time and make more effort to understand each other's needs and to interact and cooperate on common objectives, more can be accomplished.

6. Basic university courses for natural resource professionals within Hawai'i are needed. There is no real means of training natural resource managers in Hawai'i. Those active in conservation in the State are often educated in traditional biological emphases (e.g.

botany, entomology, genetics), rather than in applied science. Many who are trained in natural resource management outside of the State are not exposed to problems similar to those in Hawai'i; others do not long remain, or if they do, they often do not have adequate or current interchange with a variety of peer professionals. And many received their training decades ago. Admittedly, the number of State and Federal resource management jobs in Hawai'i to date has not been sufficient to warrant much in-State training or updating of resource professionals. However, the people charged with managing natural resources in State and Federal agencies and elsewhere could be better trained to do so, and more recently and more highly trained people are needed. Degrees in biology or business do not fully qualify one to manage a forest, although they are quite useful (see Mueller-Dombois, this volume). The disagreement (Hartwell 1985) over how to manage koa on public and private lands in Hawai'i, for example, might profit from more input from currently trained forest managers and researchers able to objectively obtain, synthesize, and apply facts about sustained yield, economics, ecosystem integrity, and biology in Hawaiian forests.

7. Conservation groups and research personnel need to become more credible and more broadly based. Hawai'i conservationists are usually outspoken, sometimes strident, and often seem sure that they possess the whole truth about what is right for Hawai'i's citizens. Conservation groups seem comprised of the same few active people and are sometimes perceived as not having much influence out of court (Ames and Stone, in press). A history of unresponsive large landowners and bureaucracies in Hawai'i, local "laid back" attitudes and disinterest, urbanization, and unemployment are undoubtedly responsible for development of some of the frustrations which conservationists feel. Unfortunately, the result has often been to polarize issues too soon and sometimes for insufficient reason. The Nature Conservancy of Hawai'i is an exception to this and has accomplished much through cooperation. Recent efforts by conservationists to inform legislators and work more with educators are encouraging but could increase.

Many conservation leaders are the people most educated about natural resource problems. Yet when researchers, teachers, and other professionals are perceived as "anti-development" advocates, objectivity can be questioned and scientific credibility can suffer. The only solution to this, as we see it, is to strive to involve more of the lay public in active conservation roles through increased awareness and incentives, and to encourage professionals to become increasingly professional. Among researchers, at least, this means less public emotion and more reliance on substantiated facts instead of opinions. Other people interested in conservation, such as private landowners, Soil Conservation Service personnel, etc., should be encouraged to join conservation groups and to play active roles to broaden the conservation base.

We believe that selection of research topics in Hawai'i could more frequently be based on critical and practical conservation problems and less often on the esoteric or "interesting." There is still a need for reconnaissance and taxonomic emphases in many forests, but there is also an increasing need for well-designed, statistically sound ecological baseline information. All are important and interrelated, of course. But too much material remains unreviewed, unpublished, and unused. Some of Hawai'i's scientists and educators could work more toward interpreting, publishing, and dispersing [our emphasis] information (Kepler, this volume). Widely circulated, peer-reviewed professional journals should be used more often, and popular articles based on studies could be better emphasized in communicating results to others. Position or issue statements by professional groups (see example in Appendix 3) could be used more effectively by scientists in Hawai'i.

Scientists in Hawai'i could probably be less actively involved in conservation leadership roles and serve more as direct factual sources for legislative, political, conservation, and educational processes. Following the successful example of The Nature Conservancy, they could also be more active as sourcepersons in community affairs and corporate boardrooms (Kepler, this volume). This sort of scientific detachment is often painful when one is frustrated by events and deeply disagrees with decisions. And we think there is a definite place for the "gadfly" and "legal adversary" in Hawai'i as elsewhere, when other approaches fail. But some results of these tactics are counterproductive in the long run. (See Juvik and Juvik 1984 for an excellent analysis of the Mauna Kea sheep/palila controversy in this regard, its effect on changing interpretation of the Endangered Species Act, and the subsequent problems.)

8. Conservation education must improve. More than any other single issue, education is the key to the future of Hawai'i's natural resource programs. Without an appreciation by legislators, politicians, and the public, of what has been discussed in this Symposium, native ecosystems will continue to deteriorate and the quality of life for Hawai'i's future citizens will be greatly diminished. Environmental education of children in primary and secondary school

systems is desirable, but we need to emphasize programs for adult decision-makers and voters. Scientists and conservationists cannot realistically inform all publics about resource problems and values, and well-informed educators are needed. The news media could provide much more in-depth, objective, enduring, and multifaceted coverage of critical conservation issues in Hawai'i, to inform and educate the public.

There are some exciting developments in conservation education in Hawai'i. Examples are the Moanalua Gardens Foundation's education program, the Living History Series, and teacher workshops; the "Science in Hawai'i" video cassettes; the keiki (children) and islandwide teacher workshops held annually at Hawai'i Volcanoes National Park; the "Puppets on the Path" environmental entertainment group; The Nature Conservancy preserve tours; Makiki Environmental Education Center; and the University of Hawai'i Hawai'i Nature Study Program. Scientists and resource managers could help educators more, by participating in teacher programs such as 'Aha Kuka (the Gathering of Councils), the annual statewide meeting for community input to the Hawai'i Department of Education on numerous topics. No environmental sponsors and only one environmental topic was listed in the 1984 program. However, many scientists are involved in other aspects of Hawai'i Department of Education programs.

Part of the job of educators is to understand the motivations of target publics. That this is a tall order is suggested in Appendix 4. Sociologists, economists, and others may need to become more involved in environmental education to increase effectiveness of conservation and other educational approaches.

The State, Federal agencies, and private groups may need to work harder here than in other locations to communicate a conservation ethic to Hawai'i's diverse ethnic groups, and to Honolulu's masses. The State could support better interpretive materials and a widely circulated magazine on renewable natural and cultural resources, for example. Yates (1984) concluded that "there is next to nothing taught in the public school system here about Hawaiian natural history." This is an overstatement, of course, but it has received national exposure. Environmental education requires money as well as good intentions, and the Governor and legislators, among others, must be convinced that it is in the people's interest (and theirs) to improve education about resource conservation issues in Hawai'i.

The loss of some of Hawai'i's brightest people to other areas cannot all be attributed to lack of local jobs. Educational opportunities in general must be improved and training upgraded, so that the old philosophy that anyone in Hawai'i can do any job is discarded. Comparisons of nationwide test scores indicate that education in Hawai'i has not yet achieved desired levels. In a survey conducted for the Hawai'i Department of Planning and Economic Development in 1984 on topics and issues relevant to public goals and policies, improving public school education led the list of citizen concerns, followed by getting more jobs and reducing crime (SMS Research 1984). Hawai'i's geographical isolation, limited size, and complicated and unique resource problems require excellence and achievement in education on a par with that desired in energy and food production.

9. The need for more cooperative efforts, on behalf of wise land use in general and native ecosystems preservation and management in Hawai'i in particular, is inescapable. To continue to try to manage development, preservation, and other uses on such a piecemeal basis is irresponsible, even if it is not intended to be so. Ecologists need to be involved in decisions about and plans for development on regional and statewide bases. Developers need to be consulted and informed about the values and uses of native ecosystem preservation. The perceptions and wishes of the public need to be systematically sampled and taken into account (perhaps while educating them more fully to the choices). Decision-makers need to act more in an atmosphere of trust and mutual respect to work out problems for the present and future. Agencies need to learn how to work more effectively together. Informed people should be better utilized in decision-making, and more informed people are needed. The mechanisms for effective cooperation are unclear, but a good start would be increased concern from influential and informed political, scientific, business, and agency leaders. To the extent that this Symposium can contribute to such progress, it will have been a success.

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APPENDIX 1.

Draft Resolution Prepared by Office of Hawaiian Affairs

REQUESTING THE RECOGNITION OF HAWAII'S NATIVE FORESTS AS A SIGNIFICANT ENVIRONMENTAL AND NATURAL RESOURCE

WHEREAS, Hawaii's native forests are becoming a limited resource, having been reduced to less than twenty-five per cent of their original range since 1778, while providing an ecosystem for rare and endangered native wildlife; and

WHEREAS, such a natural area provides a resource for education, Hawaiian culture, human enjoyment, and scientific research; and

WHEREAS, the State Plan calls for the effective protection and prudent use of the environment and other limited resources to ensure its availability to future generations as provided in the State Plan priority directions [226-105(2), HRS] and as a priority measure vital to the visitor industry [226-103(b) (5), HRS]; and

WHEREAS, the protection of the native forests provides watershed areas needed to ensure a constant water supply as well as preserving a green belt area as called for by the State Plan [226-104(c) (3), HRS];

BE IT RESOLVED that this thirteenth session of the 1985 Legislature recognizes Hawaii's native forests as a significant environmental and natural resource to be preserved.

APPENDIX 2.

Excerpts Relating to Native Ecosystems from Constitutional, Statutory, and Planning Documents

Constitution of the State of Hawai'i

Under Art IX, Public Health and Welfare, the State has "the power to promote and maintain a healthful environment, including the prevention of any excessive demands upon ... resources." Under Art IX, Conservation, Control and Development of Resources, the State has authority to "promote the development and utilization of these resources in a manner consistent with their conservation and in furtherance of ... self-sufficiency .... Each person has the right to a clean and healthful environment, as defined by laws relating to environmental quality, including ... conservation, protection, and enhancement of natural resources ... for the benefit of present and future generations".

The Hawai'i State Plan

This document is a long-range guide with a number of objectives including: 1) Prudent use of land-based, shoreline, and marine resources (Sect 11-a(1)); 2) Effective protection of unique and fragile environmental resources (Sect 11-a(2)); 3) Exercise of a conservation ethic in the use of Hawai'i's natural resources (Sect 11-b(1)); 4) Ensuring compatability between activities and natural resources and ecological systems (Sect 11-b(2)); 5) Encouraging the beneficial use of Statewide forest resources without costly or irreparable environmental damage (Sect 11-b(4)); 6) Encouraging the protection of native, rare, or endangered plant and animal species and habitats (Sect 11-b(6)); 7) Promoting the recreational and educational potential of natural resources having cultural, historical, or biological values (Sect 23-b(4)); and 8) Seeking to use limited resources wisely to ensure protection and availability for future generations (Sect 105-b).

Hawai'i County General Plan

The General Plan for the Island of Hawai'i is intended to improve the physical environment of the County for human activities; promote and safeguard the public interest; facilitate democratic determination of county policies including natural resource use; coordinate improvement and development; inject long-range consideration into short-range actions; and provide a framework for legislative and administrative decisions. The Hawai'i County General Plan addresses environmental quality in general, through policies to maintain "quality of the environment for residents" and reinforce and strengthen existing standards, and through developing ordinances to control pollution, encourage recycling, and advise the public of environmental conditions and research.

The County strives to preserve natural beauty by establishing view plane regulations in specific locations, identifying and developing viewing sites, and setting criteria to harmonize man-made elements with natural settings. It seeks to enhance natural resources and shorelines through requiring users to minimize adverse effects on the environment; encouraging a program of data collection and dissemination; and coordinating with other government agencies.

Hawai'i Revised Statutes (HRS)

Title 12, Chap 171, Sect 171-3, Department of Land and Natural Resources (DLNR), authorizes DLNR to "manage, administer, and exercise control over public lands [and to] manage and administer ... wildlife sanctuaries".

Title 12, Subtitle 4, Chap 183, Sect 183-1.5, Duties in General, requires DLNR to: "1) Gather, compile, tabulate, and publish ... information and statistics concerning the area, location, character, and increase and decrease of ... wildlife in the State"; "2) Gather and compile information ... including the care and propagation of ... wildlife for protective, productive, and aesthetic purposes"; and "6) destroy predators deemed harmful to wildlife and game".

Title 12, Subtitle 4, Chap 183, Sect 183-2, Rules, directs DLNR to "make, amend, and repeal rules for and concerning the preservation, protection, regulation, extension, and utilization of wildlife sanctuaries".

Title 12, Chap 187, Sect 187-1.2, Animal Species Advisory Commission, establishes a commission to advise the Hawai'i Board of Land and Natural Resources (BLNR) on "deliberate introduction of a species of animal by the Department into any habitat ... and any matter affecting ... wildlife conservation".

Title 12, Chap 187, Sect 187-1.3, Introduction of Species of Animals, says that "No species of animal shall be deliberately introduced by the Department ... into any habitat within the State ... unless the introduction is recommended by the forestry and wildlife division".

Title 12, Chap 187, Sect 187-1.4, Aquatic Life and Wildlife Advisory Committees, establishes advisory committes in each county to deal with "any matter affecting ... wildlife conservation ... and authorizes them to communicate its findings and recommendations to the division of forestry and wildlife".

Title 12, Chap 187, Sect 187.7, Federal aid in fish and wildlife restoration, directs the DLNR to "perform such acts as may be necessary to the coordination and establishment of cooperative ... wildlife restoration and management projects."

Title 12, Chap 187, Sect 187.13, authorizes DLNR to destroy predators ... deemed harmful to wildlife or game ... by any means deemed necessary".

Title 12, Chap 191, Sect 191.12, Permits to take Wild Birds, authorizes destruction of wild birds destructive to agriculture, or constituting a nuisance or health hazard without permits or reports.

Title 12, Chap 191, Sect 191.22, Game Management Areas, Wildlife Sanctuaries, Public History Areas, allows DLNR to "establish, maintain, manage and operate ... wildlife sanctuaries ... enter into agreements for the taking control of privately owned lands for such purposes; and adapt rules ... [for] preserving, protecting, conserving and propagating birds and mammals."

Title 12, Chap 195, Sect 195-1, Findings and Declaration of Necessity, states that "1) The State of Hawai'i possesses unique natural resources ... highly vulnerable to loss ... 2) these unique natural assets should be protected and preserved ... 3) preserves, sanctuaries, and refuges must be strengthened, and ... set aside ... and 4) that a statewide natural area reserves system should be established to preserve ... land and water areas which support natural fauna".

Title 12, Chap 195D, Sect 195 D-1, Findings and Declaration of Necessity, declares that "To insure the continued perpetuation of indigenous wildlife ... and their habitats for human enjoyment, for scientific purposes, and as members of ecosystems, it is necessary that the State take positive actions to enhance their ... survival".

Title 12, Chap 195 D, Sect 195 D-3, Determination by the Department Relating to Conservation of Particular Species, authorizes DLNR to conduct investigations on any species of wildlife ... to develop information relating to their biology, ecology, population, status, distribution, habitat needs, and other limiting factors to determine conservation measures".

Title 12, Chap 195 D, Sect 195 D-5, Conservation Programs, directs DLNR to "conduct research on indigenous wildlife ... and on endangered species and their

... ecosystems, and ... utilize the land acquisition and other authority ... to carry out programs for the conservation, management and protection of such species ... and their ecosystems". DLNR may enter into agreements with "Federal agencies and with the counties for administration and management of any area" established for the above reasons. Priority is given to endangered species and their ecosystems. DLNR must "coordinate with the natural area reserves commission and the animal species advisory commission all research, investigations, lists of indigenous and endangered wildlife ... and programs for the conservation, management, enhancement and protection" of wildlife.

Hawai'i Wildlife Plan

The following objectives are specifically related to native ecosystems:

1) Providing a basis for detailed operation plans for wildlife and wildlife habitats;

2) Recovering rare wildlife from threatened and endangered status;

3) Vigorously monitoring, retaining, and acquiring wildlife habitat for future generations of users;

4). Protecting watersheds from adverse impacts of overpopulated wildlife;

5) Resolving conflicts between exotic and native wildlife and their habitats leading to protection of the native ecosystem [our emphasis];

6) Promoting "public appreciation of the unique wildlife heritage in Hawai'i" and assisting "in public education in wildlife conservation";

7) Contributing to the development of an ecosystems approach [our emphasis] to wildlife management.

Other related State plans include Hawai'i's Renewable Resources Research Plan for the 80's (Hawai'i Department of Land and Natural Resources 1985) and, in the offing, a Threatened and Endangered Species Plan, and a State Forest and Wildlife Resource Program Plan. Federal (U.S. Fish and Wildlife Service) recovery plans are also interrelated with the Wildlife Plan.

The Hawai'i Wildlife Plan (Hawai'i Division of Forestry and Wildlife 1984) includes strategic rather than tactical plans for numerous species groups and a number of "general" plans for broad problems (e.g. Information and Education) requiring a more "holistic" approach. It also includes "special" plans (e.g. Endangered Species Preservation, and Exotic Animal/ Native Wildlife Conflicts). Items dealing with applications of these plans to native ecosystems are given below. Especially noteworthy is the realization (by DLNR also) that many of the splendid objectives are not presently attainable because of insufficient internal expertise (e.g. no Information and Education Division, no Research Division, inadequate numbers of law enforcement personnel), and insufficient funding.

The following are selected passages from General and Specific Plans within the document.

Pertinent points in the strategic Organizational Roles and Responsibilities Plan are:

> E1.c. On Conservation District zoned lands, DLNR should be the controlling or eradicating agency for newly established exotic animals determined to be pestiferous or noxious, with DOA [Hawai'i Department of Agriculture] assisting.
>
> E1.d. The responsibility for receiving, processing, screening and gathering information on proposed exotic animal importation ... should continue to rest with the DOA, with the DLNR ... in an advisory capacity.
>
> E1.h. DLNR should concentrate on wildlife status and inventory baseline information collection, distribution mapping, and recordation of species disappearance and new establishment.
>
> E1.1. DLNR should work actively with private landowners and Federal land management agencies in maintaining feral mammal populations at levels consistent with protecting watershed and ecosystem viability.

Pertinent Points in the Coordination Plan are:

> E.2.a. Specific wildlife projects, programs or problems should ... [include] consideration of not only environmental factors, but social, financial, political and land use aspects as well.
>
> E2.b. Problem solving or program planning commitments ... should be based upon sound biological truths first and other factors such as human needs and economics, second.
>
> E.2.c. From a real estate standpoint, the expenditure of funds and the implementation of the wildlife program by the Department should be prioritized as follows: 1) Unencumbered State land, 2) State land encumbered for wildlife, 3) Natural Area Reserves, 4) State land in Forest Reserve status, 5) State lands under lease or revocable permit, 6)

private lands in Forest Reserve, 7) State lands in other public uses ... , 8) Other land within the Conservation District, and 9) private or other agency lands.

E.2.e. DLNR should be prepared, with wildlife information, baseline data, maps, written policies, and manuals (which are kept up to date), to participate with other agencies in land use planning, zoning, and commitment of funds or resources so that wildlife concerns are met in the context of other interests or disciplines.

E2.f. A concerted effort should be made to modernize the statements, rules, and policies within the State structure to reflect today's realities with respect to the use of private lands for public purposes ... These could include tax incentives, differential benefits for those who dedicate lands for wildlife or wildlife users, and liability waivers which have legal "teeth". Archaic legislation should be eliminated.

Pertinent paragraphs under Wildlife Data Base Plan include:

E3.a. DLNR should not take the lead in conducting primary (basic) wildlife research activities involving detailed life history or biological studies of wildlife species, but should be active in research planning and in support of research agencies with funding, logistical assistance, and the issuance of requisite permits.

E2.b. The wildlife program element should be responsible for the application of basic survey and inventory information on population status and trends of wildlife species Statewide, with emphasis on State-owned or controlled lands ....

E3.c. Coordination should be accomplished in order to keep the wildlife data base and map file in juxtaposition with the DPED [Department of Planning and Economic Development] "Resource Base Inventory" system and other State or Federal wildlife inventory and habitat classification systems to avoid duplication and enhance accessibility.

Under Information and Education, it is stressed that Hawai'i is the only state in the nation without an information and education division or department. Without this emphasis understandings by and support of the public remain minimal and efficiency of the DLNR is reduced. Pertinent recommendations in this section of the Plan include:

> E4.a. A natural resources information and education element should be established at the Department level and should include a responsibility for the dissemination of wildlife information and providing wildlife educational assistance.

The Public Hunting Opportunities Plan encourages seeking out significant areas on State, private and Federal land to increase public hunting opportunities (F1.b.); it recommends tax incentives, surrender agreements, liability limitations, funding for capital improvement developments, lease and use fees, Federal funds, and free State services to encourage landowners to open lands to public hunting (F1.c.). It also encourages doubling of law enforcement and information and education capability at a minimum (F1.e.).

The Endangered Species Preservation Plan recommends using Recovery Teams and Plans as guidelines for all species (F2.a.); establishing a coordinating committee composed of representatives from all agencies with endangered species responsibilities, for information exchange and priority establishment (F2.b.); establishing key habitats on State lands for endangered species and acquisition where possible (F2.c.); encouraging private conservation purchases (F2.d.) and captive propagation (F2.e.); and detailed reviewing and monitoring unlisted and listed species as to status (F2.f., g.).

Recommendations under the Exotic Animal/Native Wildlife Conflicts Plan include:

> F3.a. All exotic animals should be considered potentially harmful when importations from outside the State or between islands are being prepared ....
>
> F3.b. Wherever there is a direct conflict between maintaining an exotic animal and protecting an endangered species of plant or animal and there is no alternative but to choose between the two, the policy should be to eliminate or move the exotic wildlife element.

Other recommendations (F3.c.--3.f.) are related to increasing the effectiveness of restrictions on transportation among islands (F3.c.), strengthening the importation control system by better coordination among agencies (F3.d.); better public relations (F3.e.); and tighter controls on pets, private zoos, etc. (F3.f.).

DLNR Regulation Number 4.

The (P) or Conservation Subzone has been discussed in the text. Other Subzones are:

The Limited (L) Subzone, which includes lands where human activities need to be constrained because of floods, erosion, health, or safety hazards. Lands susceptible to tsunamis, floods, volcanic activity, or landslides (slope of 40% or more) are included. Forest harvest is among the permitted uses.

The Resource (R) Subzone, which includes lands subject to development of sustained natural resource use. Parklands (national, state, county and private) and areas usable for commercial timber harvest, outdoor recreation (hunting, camping, fishing, etc.), are included, and aquaculture and commercial fishing are among the permitted uses.

The General (G) Subzone in Conservation District lands is used to designate open space with undefined conservation use but "where urban use is preventive." Farming, grazing, and gardening lands are included, and water storage and control are among the permitted uses.

Applications for permitted use in the Conservation District are reviewed by the Board of Land and Natural Resources (BLNR) which is appointed by the Governor and headed by the Chairman of DLNR. But if there is no response in 180 days, landowners may put lands to the use requested in applications. Applications must include preliminary plans for the land which are eventually to be replaced by an approved final plan.

Changes in subzone boundaries or permitted uses by landowners, agencies, or the Board necessitate a proposed amendment, notification in an appropriate newspaper, and mailing to affected landowners followed by a public hearing. The Board has the power to summon witnesses to hearings, administer oaths, and require testimony.

A number of Land Use Conditions and Guidelines and Directions are specified in Section 6 of Regulation 4. Among these are that the use allowed with the Conservation District is subject to the following:

1. It shall be compatible with the locality and surrounding areas.

2. The existing physical and environmental aspects, e.g. natural beauty and open space characteristics, shall be preserved or improved upon.

3. Deviations from conditions may be considered by the Board but shall not result in significant adverse effect to the environment.

APPENDIX 3.

A Resolution Endorsed by the 5th Pacific Science Association Inter-Congress Held in Manila, Philippines, February 3-7, 1985

RESOURCE USE CONFLICT IN HAWAII

WHEREAS, the search for alternate energy resources in the State of Hawaii has led to the use of sugarcane bagasse as a fuel for generating electricity; and

WHEREAS, with the cessation of sugarcane production in some parts of Hawaii for economic reasons, a shortage of sugarcane bagasse has recently led to the logging and woodchipping for electricity generation of the last remnant of virgin tropical lowland rainforest of Hawaii; and

WHEREAS, upon being informed of the scientific, educational, and cultural resource values of such native biota and ecological systems, the Hawaiian business community began to take measures to leave the native forest alone and turn its attention to less controversial bioenergy resources, such as non-native eucalypt trees originally planted for commercial purposes;

BE IT RESOLVED, that this meeting of the Pacific Science Association urges that publicity be given to resource use conflicts of this kind, so informed scientific opinion can be brought to bear in an effort to find means of combining natural energy resource development with good conservation practices; and

BE IT FURTHER RESOLVED, that the Pacific Science Association, through its Scientific Committee on Ecology, Conservation and Environmental Protection, monitor the progress of the important resource use issue in Hawaii, since it provides a potential model for resource development in the Pacific Basin whereby such development is carried out with due respect for environmental values and concerns.

APPENDIX 4.

Conservation, Self-Interest, and the "Real World"

One of the disturbing aspects of the Symposium to us was the polarization and antagonism of some of the participants. An example was the statement of a high-ranking State official that the "real world" is not concerned with conservation of native ecosystems, vs the statement of a University official that ecosystems shouldn't have to be justified on economic bases. We believe that both of these statements contain some truth and some error. They also highlight concerns about environmental education and human motivation.

The roles of idealism and self-interest, both useful qualities in human beings, have recently been subjected to scrutiny by 2 economists in an important book entitled Natural Resources: Bureaucratic Myths and Environmental Management (Stroup and Boden 1985). A number of thoughts and assumptions of these authors are worth considering in relation to Hawai'i's complex environmental problems: We paraphrase (with apologies to the authors) and include our own thoughts:

1. Individuals on the average [our emphasis] are motivated by self-interest. Although other motivations (concern for future generations, etc.) may enter, self-interest must be very seriously considered to motivate decision-makers in all walks of life. This includes developers, bureaucrats, and environmentalists in Hawai'i.

2. There is a cost to everything. Save a forest --give up a geothermal plant, in some cases. Trade-offs are not easy.

3. Decision-makers select options that will enhance their own welfare. Nobody wants to be wrong or unpopular or fired or ... on the average.

4. Incentives count. If the risks in choosing an option increase, it is "less likely to be selected." Enough public pressure for one land-use alternative or against another can make a difference. Rewards for preservation of ecosystems might be useful.

5. People are sensitive to shifts in costs and benefits of different choices. Everybody is after net satisfaction on the average.

6. It is rational to make decisions with less than complete information. "Ignorance makes sense!" It takes time and money to get data. The value of the information must equal the cost, or it is foolish to go

further to obtain data, especially if it doesn't usually influence decisions.

7. It is impossible to do just one thing. In ecology and economics, everything is interrelated. This, and the fact that ecology and economics are connected, is one reason for Hawai'i's complex problems.

8. Human wants usually exceed supplies. Thus, rationing systems are important and can affect greatly what there is to ration. In Hawai'i, as in many locations, we will undoubtedly need to think increasingly not only of rationing land for native ecosystems, but also for food production, cities, energy development, etc. Energy and food use, urban growth, and population size can also be rationed, of course.

There are a number of other traditional assumptions and thought patterns (mind-sets?) that are challenged in this thought-provoking volume (e.g., the "right" people with the "right" values have different goals than those with the "wrong" values, and the "right" people will accomplish more). We recommend that those interested in Hawai'i's resources--natural or man-made--and human behavior read the book to judge whether economics is truly the "dismal science", or whether we should, as the authors suggest, "design our institutions" [and interpret much human behavior?] more with self-interest in mind.

LITERATURE CITED

Ames, D.B., and C.P. Stone. In press. Problem species in Hawaii Volcanoes National Park Biosphere Reserve. Pres. Conf. Preserv. Manage. Internatl. Biosphere Reserves, Great Smoky Mtns. Natl. Park, October 1984.

Anonymous. 1985. Hawaii Natural Area Reserve System with Governor's Executive Orders (81,112 acres). Hawaii. Bot. Soc. Newsl. 24:6-7.

Armstrong, R.W., ed. 1973. Atlas of Hawaii. Dep. Geogr., Univ. Hawaii. Honolulu: Univ. Pr. Hawaii.

Balandrin, M.F., J.A. Klocke, E.S. Wurtele, and W.H. Bollinger. 1985. Natural plant chemicals: sources of industrial and medicinal materials. Science 228: 1154-1160.

Bank of Hawaii. 1984. Hawaii 1984. Annual economic report. Dep. Bus. Res. Honolulu: Bank of Hawaii.

Caufield, C. 1985. In the rainforest. New York: Alfred A. Knopf.

Chow, W.T. 1983. Urbanization: six propositions. Chap. 15. In Hawaii: a geography, ed. J.R. Morgan, 167-185. Boulder, Colo.: Westview Pr.

Clark, H. 1985. Compromise ends lawsuit over ohia logging. The Honolulu Advertiser, March 14, A-5.

Cooper, T. 1979. The Endangered Species Act: the political and environmental implications for federal agencies. Pres. 2nd Conf. Sci. Res. Natl. Parks.

County of Hawaii Planning Department. 1971. The General Plan: County of Hawaii. Hilo: County Hawaii Plan. Dep.

Degener, O. 1930. Plants of Hawaii National Park illustrative of plants and customs of the South Seas. Reprinted 1975. Ann Arbor, Mich.: Braun-Brumfield, Inc.

Forsyth, A., and K. Miyata. 1984. Tropical nature. New York: Charles Scribner's Sons.

Franklin, J.F. Design of natural area preserves in Hawaii. [This volume]

Gagne, W.C., and C.C. Christensen. Conservation status of native terrestrial invertebrates in Hawaii. [This volume]

Gomez-Pompa, A., C. Vazquez-Yones, and S. Guevera. 1972. The tropical rain forest: a nonrenewable resource. Science 177:762-765.

Gregg, W.P., Jr. 1984. The international network of biosphere reserves: a new dimension in global conservation. Pres. Miami Internatl. Symp. Biosphere, April. Miami Beach, Fla.

Handy, E.S.C., and E.G. Handy. 1972. Native planters in old Hawaii: their life, lore, and environment. B.P. Bishop Mus. Bull. 233.

Hartwell, J. 1985. Battle over koa of Kilauea: seeing the forest through the trees. The Honolulu Advertiser, March 4, A-3.

Hawaii Department of Land and Natural Resources. 1978. Regulation No. 4: a regulation of the Department of Land and Natural Resources, State of Hawaii, providing for land use within the Conservation District, providing for subzones, uses, appeals, enforcement and penalty, pursuant to Chapter 183-41, Hawaii Revised Statutes, as amended. Honolulu: State of Hawaii.

Hawaii Department of Land and Natural Resources. 1985. Hawaii's renewable resources research plan for the 80's. Honolulu: State of Hawaii.

Hawaii Department of Planning and Economic Development. 1978. The Hawaii State Plan. Honolulu: Hawaii Dep. Plan. Econ. Dev.

Hawaii Division of Forestry and Wildlife. 1984. Hawaii wildlife plan. Honolulu: Hawaii Dep. Land Nat. Resour.

Holden, C. 1985. Hawaiian rainforest being felled. Science 228(4703):1073-1074.

Holt, R.A., and B. Fox. Protection status of the native Hawaiian biota. [This volume]

Jacobi, J.D., and J.M. Scott. An assessment of the current status of native upland habitats and associated endangered species on the island of Hawaii. [This volume]

Judd, C.S. 1927. The story of the forests of Hawaii. Paradise of the Pacific 40(10):9-18.

Juvik, J.O., and S.P. Juvik. 1984. Mauna Kea and the myth of multiple use: endangered species and mountain management in Hawaii. Mountain Res. Develop. 4(3):191-202.

Kamakau, S.M. 1976. The works of the people of old. Na hana a ka poe kahiko. Trans. M.K. Pukui, Arr. and ed. D.B. Barrere. B.P. Bishop Mus. Spec. Pub. 61.

Kepler, C.B. Current and future roles of agencies, conservation groups, legislature, and the public in preserving and managing Hawaiian ecosystems: a summary. [This volume]

Kepler, C.B., and J.M. Scott. In press. Conservation of island ecosystems. Proc. 18th World Conf. Internatl. Counc. Bird Preserv. Cambridge, England.

Kirch, P.V. 1982. The impact of the prehistoric Polynesians on the Hawaiian ecosystem. Pac. Sci. 36(1):1-14.

Lamoureux, C.H. Restoration of native ecosystems. [This volume]

Lawrence Berkeley Laboratory, California. 1981. Geothermal energy for Hawaii: a prospectus. Prep. W.W.S. Yen and D.S. Iacofano for U.S. Dep. Energy. Honolulu: Hawaii Dep. Plan. Econ. Develop.

Lockwood, J.P. 1985. Ohia chipping--image, reality. Hawaii Tribune-Herald, June 18, 4.

Loope, L.L., and C.P. Stone. 1984. Introduced vs native species in Hawaii: a search for solutions to problems of island biosphere reserves in Hawaii. Proc. 1st Internatl. Biosphere Congr., 252-257. Minsk, Byellorussia: U.S.S.R.

Malo, D. 1951. Hawaiian antiquities (Moolelo Hawaii). 2nd ed. Transl. N.B. Emerson, 1898. B.P. Bishop Mus. Spec. Pub. 2.

Morgan, J.R. 1983. Tourism. Chap. 11. In Hawaii: a geography, ed. J.R. Morgan, 117-131. Boulder, Colo.: Westview Pr.

Mueller-Dombois, D. Ohia dieback and protection management of the Hawaiian rain forest. [This volume]

Myers, N. 1980. Conversion of tropical moist forests. Rep. Comm. Res. Priorities Trop. Biol. Washington, D.C.: Natl. Acad. Sci.

Myers, N. 1984. The primary source: tropical forests and our future. New York: W.W. Norton & Co.

Newman, A. 1984a. Conservation update. Elepaio 44(9):92-93.

Newman, A. 1984b. No na leo ole. Elepaio 45(6):51-52.

Office of Hawaiian Affairs. 1984. Office of Hawaiian Affairs culture plan (Draft). Honolulu: Off. Hawn. Affairs. Typescript.

Oldfield, M.L. 1984. The value of conserving genetic resources. Natl. Park Serv., Washington, D.C.

Olson, S.L., and H.F. James. 1982. Prodromus of the fossil avifauna of the Hawaiian Islands. Smithson. Contrib. Zool. 365.

Peterson, F. 1983. Water resources. Chap. 8. In Hawaii: a geography, ed. J.R. Morgan, 73-87. Boulder, Colo.: Westview Pr.

Porter, R.D., and D.B. Marshall. 1976. The recovery team approach to restoration of endangered species. Proc. Internatl. Conf. Birds of Prey, Vienna, 314-319.

Schonewald-Cox, C. Genetics, minimum population size, and the island preserve. [This volume]

Scott, J.M., C.B. Kepler, and J.L. Sincock. Distribution and abundance of Hawaii's endemic land birds: conservation and management strategies. [This volume]

SMS Research. 1984. The 1984 Hawaii State Plan survey. Prep. for Hawaii Dep. Plan. Econ. Develop. Honolulu: SMS Research.

Spoehr, H. 1984. Resource management; a native Hawaiian tradition. Trans. 24th Ann. Hawaii For. Wildl. Conf., 43-54. Honolulu.

Stannard, D.E. 1985. Tourism and the destruction of Hawaii. Save Hawaii, June,

Stoel, T. 1980. Save the rain forests. IUCN Bull. New Ser. 11(5):17-18, 22-26.

Stone, C.P., and D.B. Stone. 1984. The "10 most-wanted" management actions for terrestrial Hawaiian ecosystems: a survey. Elepaio 45:41-48.

Street, J. 1983. Soils. Chapter 9. In Hawaii: a geography, ed. J.R. Morgan, 89-97. Boulder, Colo.: Westview Pr.

Stroup, R.L., and J.A. Baden. 1983. Natural resources: bureaucratic myths and environmental management. Pacific Stud. Pub. Policy. Cambridge, Mass.: Ballinger Pub. Co.

Sun, M. 1985. Host of problems threaten national parks: Park officials, legislators, and environmentalists take stock and suggest solutions. Science 228 (4706):1413-1414.

U.S. Congress. 1973. Endangered species act of 1973. 93rd Congr., Dec.

U.S. Department of Energy. 1982a. Geothermal power development in Hawaii. Vol. 2. Infrastructure and community services requirements--island of Hawaii. Honolulu: Hawaii Dep. Plan. Econ. Develop.

U.S. Department of Energy. 1982b. Geothermal power in Hawaii. Vol. 1. Review and analysis. Honolulu: Hawaii Dep. Plan. Econ. Develop.

U.S. Department of State. 1980. The world's tropical forests: a policy, strategy, and program for the United States. Dep. State Pub. 9117, Internatl. Org. Conf. Ser. 145. Washington, D.C.

Weisburd, S., and J. Raloff. 1985. Climate and Africa: why the land goes dry. Sci. News 127:282-285.

Wydoski, R.S. 1977. Realistic management of endangered species--an overview. Proc. West. Assn. State Game Fish Comm. 57, 273-301.

Yates, S. 1984. On the cutting edge of extinction. Audubon 86(4):62-85.

Zimmerman, E.C. 1963. Nature of the land biota. In Man's place in the island ecosystem: a symposium, ed. F.R. Fosberg, 57-65. Tenth Pacific Sci. Conf., 1961. Honolulu: Bishop Mus. Pr.

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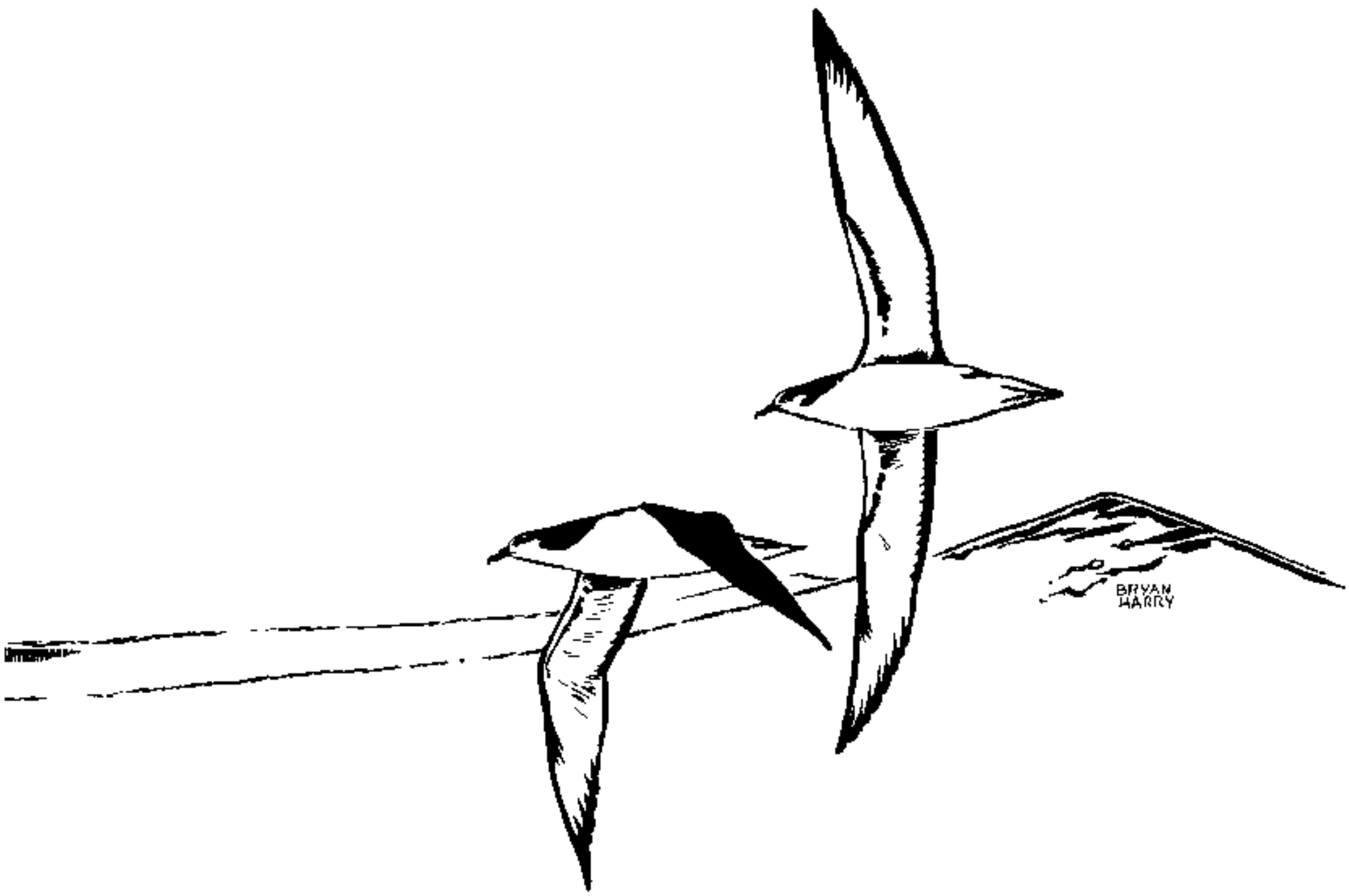

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