Technical Report HCSU-046

PALILA RESTORATION RESEARCH, 1996–2012

Paul C. Banko[1] and Chris Farmer[2], Editors

[1]U.S. Geological Survey, Pacific Island Ecosystems Research Center, Kīlauea Field Station,
P.O. Box 44, Hawaii National Park, HI 96718
[2]American Bird Conservancy, Kīlauea Field Station,
P.O. Box 44, Hawaii National Park, HI 96718

Hawai'i Cooperative Studies Unit
University of Hawai'i at Hilo
200 W. Kawili St.
Hilo, HI 96720
(808) 933-0706

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PALILA RESTORATION RESEARCH, 1996–2012

A palila (*Loxioides bailleui*) selects a seedpod from a māmane (*Sophora chrysophylla*) tree high on the western slope of Mauna Kea, Hawai'i. The palila's ecology and existence are inextricably linked to green māmane seeds, their critically important food. Chronic shortfalls in the supply of māmane seedpods could lead to the extinction of the palila. Photo by Jack Jeffrey (http://www.jackjeffreyphoto.com/).

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INTRODUCTION

Paul C. Banko, Luanne Johnson, Steve J. Dougill, Chris Farmer

The Palila Restoration Project was initiated in 1996 by the U.S. Geological Survey to assist government agencies mitigate the effects of realigning Saddle Road (Highway 200) through Palila Critical Habitat (U.S. Fish and Wildlife Service 1998, Federal Highway Administration 1999). Ecological research on the palila (*Loxioides bailleui*), an endangered Hawaiian forest bird, carried out by the U.S. Geological Survey (formerly organized as the Research Division of U.S. Fish and Wildlife Service) since 1987 and research conducted by the Palila Restoration Project provided the scientific bases for developing a recovery strategy (U.S. Fish and Wildlife Service 2006) and its adaptive implementation.

The main objectives of the Palila Restoration Project were to develop techniques for reintroducing the palila to a portion of its former range, investigate the biological threats to the palila and its habitat, and synthesize the existing body of ecological knowledge concerning the palila. Five broad study themes formed the research framework:

1. Population reintroduction and restoration
2. Demography and breeding ecology
3. Habitat use and food ecology
4. Vegetation ecology
5. Predator ecology and management

An element that was not included in the research program of the project was the ecology and management of introduced ungulates, which has historically constituted the single greatest threat to Palila Critical Habitat (Banko *et al.* 2009). The absence of ungulate studies should not be interpreted to mean that we believe ungulates no longer damage palila habitat. Other research has already established that removing alien browsers and grazers from Mauna Kea is essential for the recovery of the subalpine forest on which palila now depend (Scowcroft and Giffin 1983; Scowcroft and Sakai 1983; Scowcroft and Conrad 1988, 1992; Hess *et al.* 1999). Moreover, the Federal District Court of Hawai‘i has ordered the state of Hawai‘i to remove browsing ungulates from Palila Critical Habitat (Banko *et al.* 2009, Hess and Banko 2011).

This final report summarizes results of Palila Restoration Project research from December 1996 to December 2012. Even though some results contained in this report have been published in scientific journals and other technical reports (Appendix I), they are included here to provide a comprehensive chronicle of all project activities.

Synopsis of Palila Biology and Conservation

Palila occurred prehistorically at low elevation on O‘ahu and Kaua‘i (Olson and James 1982, Burney *et al.* 2001), but historically they were found only on Hawai‘i Island where they were restricted to the slopes of Mauna Kea and portions of Hualālai and Mauna Loa (Banko *et al.* 2002a). Due mainly to habitat loss from ungulate browsing, palila have declined in abundance and distribution and are now only found in about 5% of their historical range on the upper slopes of Mauna Kea (Scott *et al.* 1986, Banko *et al.* 2013). Here, the relatively dry, subalpine forest of māmane (*Sophora chrysophylla*) and naio (*Myoporum sandwicense*) supports a small and annually fluctuating population, which at its peak during 1998–2012 was estimated to be 6,463 individuals in 2003 (Camp and Banko 2012).

The population has increasingly become restricted to the western slope of Mauna Kea (Jacobi *et al.* 1996, Camp and Banko 2012). Like most other endangered Hawaiian forest birds, palila are found today only in the upper limit of their former range where habitat conditions may always have been marginal. Annual fluctuations in numbers and the concentration of nesting within about 10 km^2 of habitat make palila highly vulnerable to extinction. Palila show strong site fidelity (Fancy *et al.* 1993), and individual palila nest in the same general location year after year (Banko *et al.* 2002a).

Palila depend on māmane trees for immature seeds, flowers, leaf buds, and insects (Banko *et al.* 2002a). Annual variation in māmane seed pod production affects palila survival, and palila attempt fewer nests and produce fewer chicks in years of relatively low māmane pod production (Lindsey *et al.* 1995, Banko *et al.* 2002a). Māmane is heavily browsed by feral sheep (*Ovis aries*) and European mouflon sheep (*O. gmelini musimon*), but the culling of these populations by hunters and Hawai'i Division of Forestry and Wildlife has allowed some māmane regeneration (Hess *et al.* 1999).

Palila habitat has also been invaded by introduced annual grasses and other weeds, resulting in the accumulation of fire fuels in some areas. The threat of fire has been a longstanding concern for the survival of the palila.

In some areas of Palila Critical Habitat, such as on the eastern slope of Mauna Kea, the belt of māmane forest has been narrowed by long-term cattle ranching and feral ungulate browsing. Because the timing of seed set varies with elevation, the seasonal availability of māmane seeds has shortened as forest width has narrowed (Banko *et al.* 2002b). Although narrow bands of forest may support palila populations during years when seed crops are large, there are few alternate food resources available when seed crops are small. Therefore, the width of the forest belt and the density of trees are important considerations when planning reintroduction and recovery programs.

Predation by feral cats (*Felis catus*) reduces palila nesting success and survival (Banko *et al.* 2002a, Hess *et al.* 2004). Rats (*Rattus rattus*), which are more abundant where naio trees are co-dominant with māmane (Amarasekare 1994), also destroy some palila nests (Banko *et al.* 2002a). Even low rates of predation by small mammals, in combination with high nest and roost site fidelity by palila, might reduce the persistence and productivity of small populations. Therefore, reducing predation may be important when enhancing or re-establishing palila outside the core breeding area.

The palila is an appropriate candidate for which to develop and apply restoration techniques because: (1) the species probably cannot be recovered without active and timely management (Banko *et al.* 2009); (2) adequate information on palila ecology exists to guide management efforts (van Riper *et al.* 1978; van Riper 1980a, 1980b; Pletschet and Kelly 1990; Fancy *et al.* 1993; Jeffrey *et al.* 1993; Lindsey *et al.* 1995; Jacobi *et al.* 1996; Fancy *et al.* 1997; Banko 2009); and (3) techniques developed for palila recovery may be applicable to recovering other Hawaiian forest birds. Another advantage to working with palila is that they can carry radio transmitters large enough to permit monitoring for up to eight weeks, which can facilitate the evaluation of management activities. In addition, avian malaria and pox are essentially absent in the palila population and are not likely to complicate the interpretation of management treatments. Finally, it is possible to develop management techniques when levels of inbreeding are low and unlikely to impede population restoration (Fleischer *et al.* 1994).

Personnel

The project team (Appendix II) consisted of the project leader and technical and administrative staff employed through the University of Hawai‘i at Mānoa (Pacific Cooperative Studies Unit) or the University of Hawai‘i at Hilo (Hawai‘i Cooperative Studies Unit). In addition to salaried staff, hundreds of interns assisted with field and laboratory investigations. Groups of interns consisted of university students or recent graduates. In return, they received professional training and experience.

Study Areas

We studied eight relatively dry, montane to subalpine woodland sites where palila studies had been conducted since 1987 or where palila might eventually be reintroduced (Figure I.1). These study sites are referred to in most chapters of this report, often without reprinting a map. Sites on the western slope of Mauna Kea where palila were most abundant and nested most frequently were Pu‘u Lā‘au Mauka (PL Mauka) and Pu‘u Lā‘au Makai (PL Makai). Manao and Ahumoa were sites on western Mauna Kea where palila were less abundant and nested less frequently. Three potential reintroduction sites on Mauna Kea where palila were absent or rare were North, South, and Pōhakuloa Flats (PFlats). Another possible reintroduction site was located on Mauna Loa (Kīpuka ‘Alalā). Pōhakuloa Flats (also known as Training Areas 1 and 2) and Kīpuka ‘Alalā (also known as Training Area 23) were located within the U.S. Army’s Pōhakuloa Training Area. The other sites were located on state lands managed as forest reserve or game management areas by the Hawai‘i Division of Forestry and Wildlife. Research was conducted within a grid of transects at each of the western slope study sites (Figure I.2). At proposed reintroduction sites, we initially worked along one or two transects which paralleled roads. In 1998, we established a grid system of transects at the northern site to facilitate translocation and predator control and research (Figure I.3).

The study sites encompassed a wide range of elevation, extending from 1,701–2,835 m (5,580–9,300 ft; Table I.1). Annual rainfall averaged 500–1,000 mm at all sites. Annual rainfall averaged 511 mm (58-year record) at PL Mauka and PL Makai and surrounding areas (Juvik *et al.* 1993). North potentially was the wettest site; followed closely by the other reintroduction sites. There was a distinct rainfall gradient at PFlats, which resulted in about 35% more precipitation in the eastern portion compared to the western portion. All sites were dominated by native trees, generally less than 3–10 m tall, and shrubs (Hess *et al.* 1999). Native grasses were present in all areas, but alien grasses generally dominated.

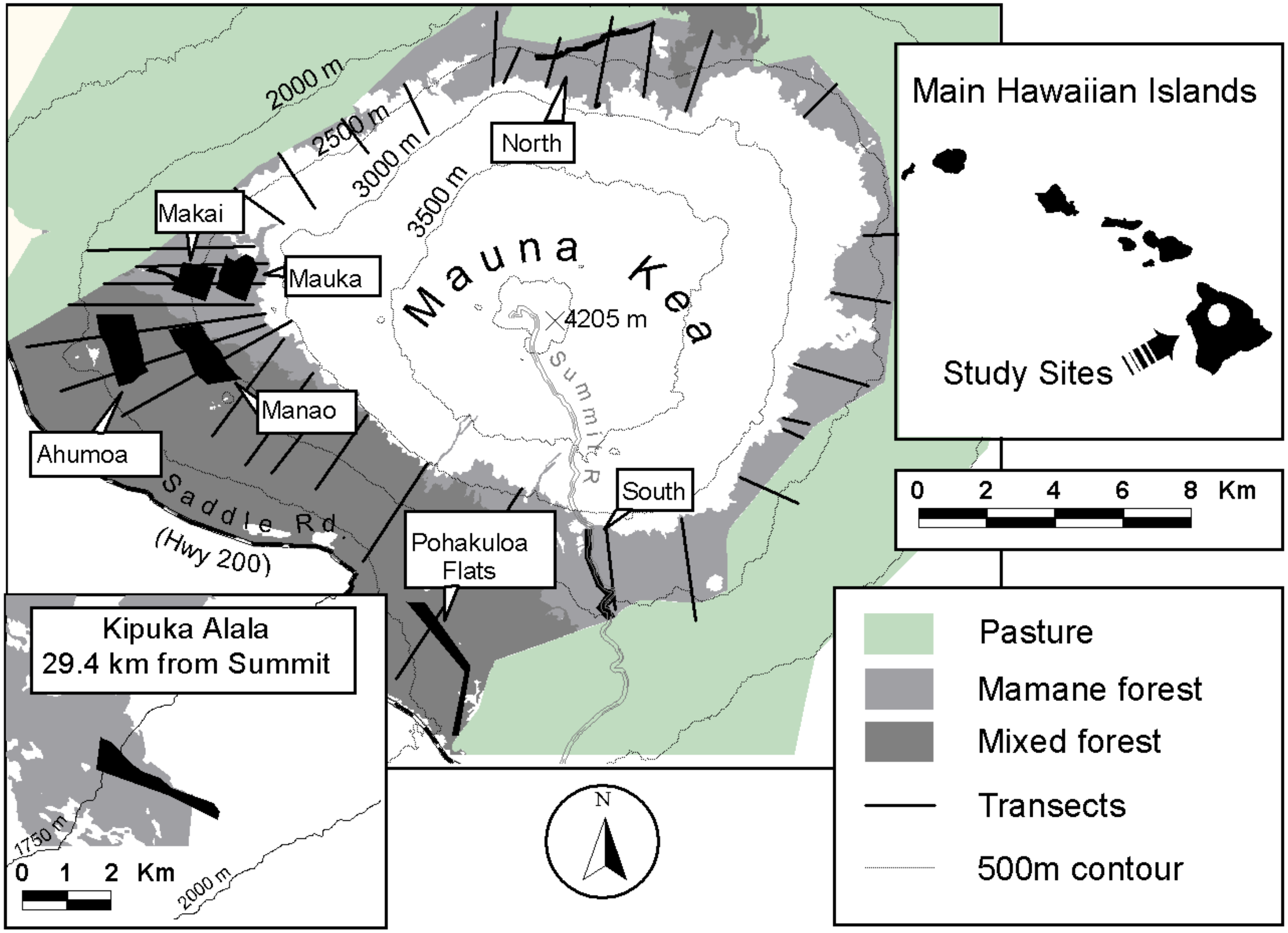

Figure I.1. Locations of eight study sites and 32 transects on Mauna Kea and Mauna Loa. Mauna Kea study sites were located within Palila Critical Habitat in Mauna Kea Forest Reserve (MKFR) and Kaʻohe Game Management Area (Ahumoa). Kīpuka ʻAlalā was situated on Mauna Loa within Pōhakuloa Training Area (PTA) and Pōhakuloa Flats was within MKFR and PTA.

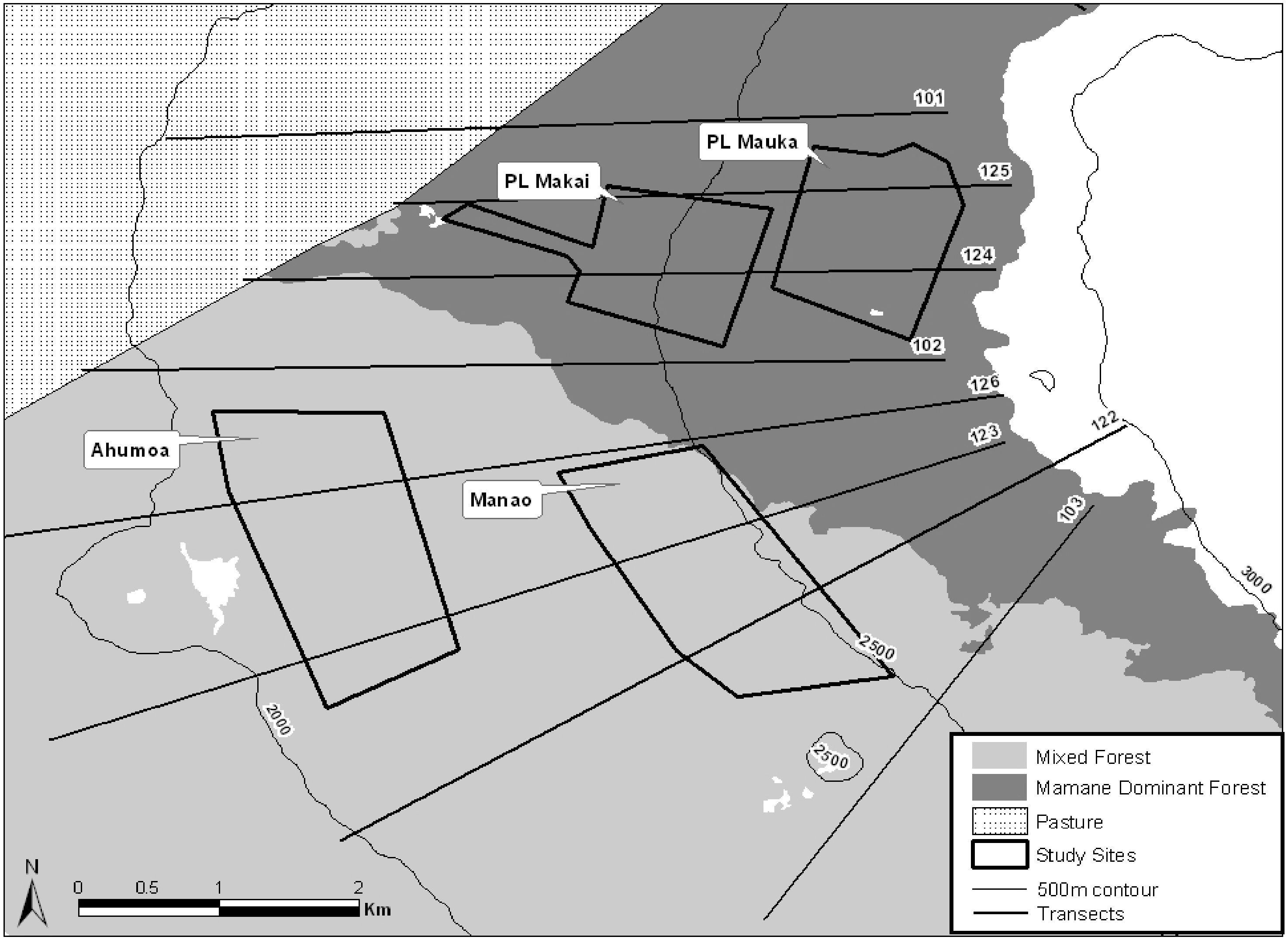

Figure I.2. Study sites and transects on the western slope of Mauna Kea. Transects 101–103 were established by the Hawai'i Forest Bird Survey (Scott *et al.* 1986), and transects 122–126 were established by the Palila Restoration Project in 1998.

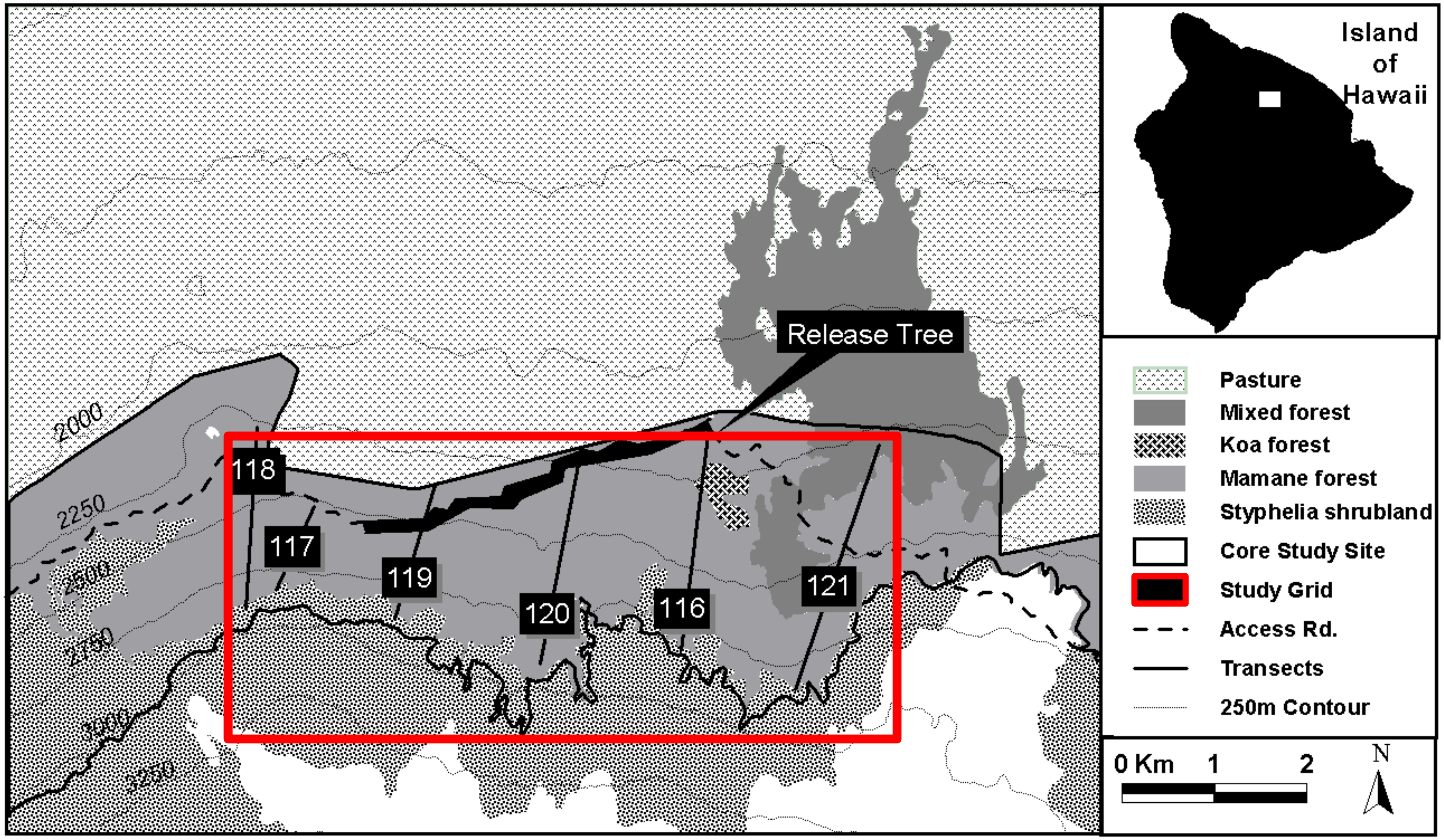

Figure I.3. Transects and habitat where translocated palila were released on the northern slope of Mauna Kea, Hawai‘i, 1997–2006. Transects 116–117 were established by the Hawai‘i Forest Bird Survey (Scott *et al.* 1986), and transects 118–121 were established by the Palila Restoration Project in 1998. *Styphelia* now is *Leptocophylla*.

Table I.1. Elevation and palila population status at study sites.

Study site	Range of elevation	Palila population status
Pu'u Lā'au Mauka	8,500–9,200 ft 2,591–2,804 m	High
Pu'u Lā'au Makai	7,500–8,500 ft 2,286–2,591 m	High
Manao	7,500–8,300 ft 2,286–2,530 m	Intermediate – low
Ahumoa	6,800–7,360 ft 2,073–2,243 m	Intermediate – low
North	6,900–8,400 ft 2,103–2,560 m	Absent since 1970s
South	8,080–9,300 ft 2,463–2,835 m	Very low
Pōhakuloa Flats	6,580–6,650 ft 2,006–2,027 m	Absent since 1970s
Kīpuka 'Alalā	5,580–6,270 ft 1,701–1,911 m	Absent since 1950s

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55. Farmer, C., K. W. Brinck, and P. C. Banko. 2008. Forest structure and composition on Mauna Kea, Hawai‘i. 2008 Hawai‘i Conservation Conference, 29–31 July 2008, Honolulu, HI. (Poster)

56. Leonard, D. L., Jr., P. C. Banko, K. W. Brinck, C. Farmer, R. J. Camp, and J. Nelson. 2008. Palila population plummets. 2008 Hawai‘i Conservation Conference, 29–31 July 2008, Honolulu, HI. (Poster)

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58. Farmer, C., K. W. Brinck, and P. C. Banko. 2008. Fifteen-year nesting study of a Hawaiian honeycreeper. Combined annual meeting of American Ornithologists' Union, Cooper Ornithological Society, and Canadian Society of Ornithologists, 4–8 August 2008, Portland, OR. (Poster)

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65. Banko, P. C. 2011. Feeding specialization and the vulnerability of Hawaiian forest birds to food web disruption and environmental change. Symposium on Evolution of Life on Pacific Islands and Reefs: Past, Present, and Future. Smithsonian Institution and National Tropical Botanical Garden, 26–30 May 2011, Honolulu, HI. (Oral)

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68. Banko, P. C., R. J. Camp, C. Farmer, K. W. Brinck, D. L. Leonard, and R. M. Stephens. 2012. Response of a Hawaiian subalpine, dry forest bird community to prolonged drought and habitat degradation by feral ungulates. 2012 Hawai‘i Conservation Conference, 31 July–2 August 2012, Honolulu, HI. (Invited Oral)

69. Banko, P., J. Juvik, S. Juvik, J. Jacobi, P. Scowcroft, C. Farmer, K. Brinck, R. Camp, D. Leonard, and R. Stephens. 2012. Mauna Kea and the myth of multiple use, revisited. Vulnerable Islands in the Sky: Science and Management of Tropical Island Alpine and Sub-Alpine Ecosystems International Symposium, 4–7 August 2012, Waimea, HI. (Invited Oral)

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Appendix II: Project Staff Roster

Project Management:

1996–2012	**Paul Banko**, PhD. Project leader. Research planning, interpretation, management, and coordination.
1999–2004	**Julie Leialoha**. Project coordinator. Interagency coordination and planning; community outreach; supervision of vegetation research.
2002–2003	**Steven Hess**, PhD. Project manager. Field research planning and management; data analysis and interpretation; report preparation; GIS.
2004–2009	**Chris Farmer**, PhD. Project manager. Field research planning and management; data analysis and interpretation; report preparation; geographic information system (GIS).

Data Management and Analysis:

1998–1999	**Elizabeth Gray**, PhD. Quantitative ecologist. Supervision of data management, analysis, and interpretation.
1998–2001	**Megan Laut**, MSc. Data technician. Data entry and management; report preparation.
1998 –2005	**Barbara Muffler**. Data technician. Data entry and management; literature management; administration.
1999–2000	**Heather Weddle**. Data clerk. Data entry; literature entry; administration.
2002–2009	**Kevin Brinck**, MSc. Quantitative ecologist. Statistical analysis and interpretation of data; research design; geographic information system (GIS).
2003–2005	**Kelly Kozar**. Data technician. Data entry and management; report preparation; geographic information system (GIS).
2004–2007	**Sarah Nash**, MSc. Data technician. Data entry and management; report preparation; geographic information system (GIS); administration.

Bird Studies (translocation; nesting biology; banding and radio-tracking; population monitoring):

1996–2001	**Luanne Johnson**. Field leader. Supervision of ornithological research; logistical planning; data collection, analysis, and management; field safety.
1997–1999	**John David Semones**. Ornithologist. Data collection, analysis, and management; intern supervision.
1997–2000	**Michael Wiley**. Ornithologist. Data collection, analysis, and management; intern supervision.
1999	**Kendy Radasky**. Ornithologist. Data collection; intern supervision.

1999–2000	**Rachael Rounds**. Ornithologist. Data collection; intern supervision.
2000–2002	**David Cerasale**. Ornithologist. Data collection; intern supervision.
1999–2004	**Colleen (Murray) Cole**. Field leader. Supervision of ornithological research; logistical planning; data collection, analysis, and management; field safety. Data and administrative clerk. Data entry and management; report preparation; administration.
2001–2003	**Susan Marshall**. Ornithologist. Data collection; intern supervision.
2002–2003	**Brittany Cline**. Ornithologist. Data collection; intern supervision.
2002–2004	**Andrea Lindo**. Ornithologist. Data collection; intern supervision.
2003–2005	**Emily Severson**. Ornithologist. Data collection; intern supervision.
2003–2004	**Grant Beauprez**, MSc. Field leader. Supervision of ornithological research; logistical planning; data collection, analysis, and management; field safety.
2003–2005	**Julie (Castner) Danner**. Ornithologist. Data collection; intern supervision.
2003–2004	**Corinna Hanson**. Field technician (temporary hire).
2004–2006	**Bobby Hsu**. Ornithologist. Data collection; intern supervision.
2005–2006	**Robert Stephens**, MSc. Field leader. Supervision of ornithological research; logistical planning; data collection, analysis, and management; field safety.
2005–2006	**Bridget Frederick**. Ornithologist. Data collection; intern supervision.
2006–2007	**Carter Snow**. Ornithologist. Data collection; intern supervision.
2006–2007	**Jeremy Morris**. Ornithologist. Data collection; intern supervision.

Insect Studies (avian diet composition; distribution and life history of māmane moths; biology of caterpillar parasitoids; distribution and impacts of yellowjackets and ants):

1996–2001	**Peter Oboyski**, MSc. Field leader. Supervision of entomological research in field and laboratory; research and logistical planning; data collection, analysis, and management; field safety.
1998	**Mathew Kweskin**. Entomologist. Data collection, management, and analysis; intern supervision.
1999–2002	**John Slotterback**. Entomologist. Data collection, management, and analysis; intern supervision.
2000–2002	**Aaron Gregor**. Entomologist. Data collection, management, and analysis; intern supervision.

2002–2005	**David Pollock**, MSc. Field leader. Supervision of entomological research in field and laboratory; research and logistical planning; data collection, analysis, and management; field safety.
2004–2006	**Marla Schwarzfeld**. Entomologist. Data collection, management, and analysis; intern supervision.
2005	**Katherine Kieler**. Entomologist. (temporary hire)

Predator Studies (biology and impacts of small mammals and raptors; control of alien predators):

1997–2003	**Dan Goltz**, MSc. Field leader. Supervision of predator research and control; data collection, analysis, and management.
1999–2000	**Chris Murray**. Wildlife biologist. Data collection, analysis, and management; intern supervision.
2000–2002	**Alison (Agnes) Polanski**. Wildlife biologist. Data collection, analysis, and management; intern supervision.
2002–2005	**Raymond Danner**. Field leader. Supervision of predator research and control; logistical planning; data collection, analysis, and management.
2004	**George Parish**. Field technician. (temporary hire)
2004–2005	**Daniel Nelson**. Field leader. Supervision of predator research and control; logistical planning; data collection, analysis, and management; field safety.
2004–2005	**Jacob Scheidler**. Field technician. (temporary hire)

Vegetation Studies (composition and structure of subalpine vegetation; distribution and impacts of weeds; habitat requirements of birds):

1996–2002	**Steve Dougill**. Botanist. Supervision of vegetation research; logistical planning; data collection, analysis, and management; geographical information system (GIS).
1999	**Traci (Rogers) Semones**. Botanist. Data collection, analysis, and management; intern supervision.
1999–2001	**Laurie Gold**. Botanist. Data collection, analysis, and management; intern supervision.
2004–2009	**Kalei Rapozo**. Botanist. Phenology coordinator; data collection, analysis, and management.
2004–2005	**Jennifer (Crummer) Higashino**. Botanist. Forest restoration coordinator; supervision of vegetation research; community outreach.
2008	**Jennifer Tietjen**. (temporary hire)

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SECTION I: POPULATION REINTRODUCTION AND RESTORATION

Preface

The major goal of our research was to develop methods for restoring the palila population. Most of our effort focused on testing techniques for reintroducing palila into former range where habitat restoration could be accelerated and predators could be controlled. Our first task was to evaluate sites where we could reintroduce palila, as described in Chapter 1. We evaluated four sites (three on Mauna Kea and one on Mauna Loa) by comparing their assets and liabilities to those of four sites on western Mauna Kea, where most of the palila population was located. We assessed habitat quality in terms of environmental gradients, vegetation structure, species composition, and recruitment of māmane. We also evaluated the availability of food, particularly māmane pods but also caterpillars and other insect prey, and threats from predators, diseases, wildland fire, and human disturbance. We identified the northern slope of Mauna Kea as having the best characteristics for reintroducing palila.

Our approach to reintroducing palila to northern Mauna Kea was to translocate wild palila from the western slope to the Pu'u Mali area. As reported in Chapter 2, we conducted six trials during which 188 birds were translocated. Although many palila returned to the western slope, some nested successfully on the northern slope, eventually producing progeny that also nested successfully.

We also investigated other potential ways for restoring palila populations. To investigate methods for bolstering the survival and productivity of palila, we provided supplemental food to palila nestlings and their parents. As discussed in Chapter 3, our limited efforts were not successful. In addition to translocation, harvesting wild eggs for rear-and-release or captive breeding are potential methods for reintroducing and bolstering palila populations. In Chapter 3, we describe the results from harvesting palila eggs from wild pairs and monitoring the effect of egg harvest on subsequent reproduction. In support of a separately-funded program, we monitored the survival and behavior of captive-reared palila that were released near Pu'u Mali, as explained in Chapter 4.

Chapter 1. Evaluating Sites for Palila Reintroduction. Paul C. Banko, Chris Farmer, Luanne Johnson, Steve J. Dougill, Peter T. Oboyski

Chapter 2. Translocating Wild Palila. Paul C. Banko, Chris Farmer, Kevin W. Brinck, Luanne Johnson

Chapter 3. Harvesting Wild Eggs and Supplementing Food at Nests. Paul C. Banko, Luanne Johnson, Steve J. Dougill

Chapter 4. Release and Monitoring of Captive-reared Palila. Chris Farmer, Paul C. Banko

1 EVALUATING SITES FOR PALILA REINTRODUCTION

Paul C. Banko, Chris Farmer, Luanne Johnson, Steve J. Dougill, Peter T. Oboyski

Introduction

We evaluated eight sites for their suitability for palila (*Loxioides bailleui*) reintroduction during 1996–2002 (see Introduction). Four sites (PL Mauka, PL Makai, Manao, and Ahumoa) on the western slope of Mauna Kea, Hawai‘i, support the main population of palila, while at the other sites palila are rare (South) or absent (North, PFlats, Kīpuka ‘Alalā; Figure I.1, Table I.1). Our main objectives were to evaluate the sites with reference to PL Mauka and PL Makai, where palila are most common. We report here on two major aspects of habitat quality: forest composition, structure, and recruitment; and availability of food resources from māmane (*Sophora chrysophylla*), an endemic tree. Elsewhere in the report, we use a different spatial stratification to consider these two topics and other important habitat factors, including alien weeds, threats to food resources, predator abundance, and disease.

Forest Composition, Structure, and Recruitment

The composition and structure of habitat is fundamentally important to palila restoration. The forests on Mauna Kea, and elsewhere in the species' historic range, have deteriorated over a century and a half due to feral ungulates (Warner 1960). Palila would likely have become extinct decades ago had it not been for the removal of many thousands of animals during the 1930s and 1940s (Bryan 1947, Tomich 1986). More recent culling of feral ungulate populations has resulted in additional māmane recruitment. Māmane saplings are used sparingly by palila, but as they become larger trees they will provide the resource base necessary for population expansion. Our goal was to determine forest characteristics at candidate reintroduction sites to evaluate their ability to support palila populations.

Availability of Māmane Food Resources

We monitored resources used by palila to determine the importance of seasonal trends in food abundance and distribution as potential factors limiting palila populations. Palila feed primarily on the seeds, flowers, and new foliage of the māmane tree, as well as on *Cydia* caterpillars found inside māmane seeds. Māmane phenology varies with elevation, which allows palila to persist where they can track seasonal shifts in flower, pod, and insect abundance across a wide range of elevation (Scott *et al*. 1984, Fancy *et al*. 1993, Lindsey *et al*. 1995, Banko *et al.* 2002). On Mauna Kea, palila densities are positively correlated with the number of māmane pods at different elevations (Hess *et al*. 2001). Additionally, palila concentrate in areas containing many large, mature māmane trees (van Riper *et al*. 1978). Thus, the relative scarcity of palila on the southern, eastern, and northern slopes may reflect more limited food resource availability due to smaller forest size, limited elevation gradient, more fragmented landscape, or the small size of regenerating trees.

To evaluate food availability throughout the year on Mauna Kea, we monitored māmane tree phenology and productivity monthly at sites on the western, southern, and northern slopes. By combining these data with indices of māmane tree density gathered in 1995–1996, we were able to determine relative availability of food resources per unit area across the existing range of palila habitat.

Methods

Forest Composition, Structure, and Recruitment

We used the point-centered quarter method, a transect-based distance method (Mueller-Dombois and Ellenberg 1974), to estimate densities of trees and saplings at the eight sites from 1995–1996. At each site we randomly selected 24–30 point-centers along the transect. At the North and South sites, 24 points were sampled. At PFlats, 28 points were sampled, while at Kīpuka ʻAlalā and the four western slope sites, 30 points were sampled. Within four quarters centered on each point, we selected the nearest mature tree with crown size greater than 2 m in height and width and also the nearest sapling tree with crown height and width less than 2 m, but greater than 0.5 m. We measured the distance (± 0.5 m) from each selected tree or sapling crown center to the sample point. All conspecific stems emerging from the ground within 1-m radius of the selected individual were considered to be from the same individual. Tree densities were calculated with Pollard's (1971) formula for an unbiased population density estimate of the point-centered quarter method, where N_P = the population density estimate, n = the number of random points, and r_{ij} = the distance from the random point i to the nearest tree of interest in quadrant j:

$$N_P = 4(4n - 1) / \pi \Sigma (r^2_{ij}) \qquad \text{(Equation 1)}$$

Availability of Māmane Food Resources

We assessed māmane phenology monthly on the western slope of Mauna Kea from 1989–2002 along designated transects in the core study areas of PL Mauka and PL Makai (māmane-dominant forest) and from 1991–2002 in the core study areas of Ahumoa and Manao (naio-dominated, mixed naio-māmane forest; Table 1.1). In 1996, we established additional transects on the northern and southern slopes of Mauna Kea, as well as two sites within Pōhakuloa Training Area at PFlats (Training Areas 1 and 2 combined) and Kīpuka ʻAlalā (Training Area 23). In March of 1999, we modified our sampling protocol to also assess phenology of randomly selected māmane trees along Hawaiʻi Forest Bird Survey transects on the western, northern, southern, and eastern slopes of Mauna Kea (see Chapter 16: Food Availability: Māmane Phenology). We discontinued our original sampling protocol at the North site, the South site, and Kīpuka ʻAlalā after February 1999 and at PFlats after December 2001 (Table 1.1). Because the new protocol differed from our previous surveys, the results from randomly selected trees are not presented in this chapter.

We evaluated the phenology of individually marked trees every month at stations placed 150 m apart along transects. We recorded the number of pods and flowers per tree, as well as the percent of live branch tips with pods, flowers, and new foliage flush. We also collected two randomly selected pods (each >3 mm wide) from each study tree to determine the frequency of *Cydia* caterpillar infestation. We determined caterpillar presence by dissecting each pod and recording the number of seeds per pod, the percentage of pods with *Cydia*, and the percentage of seeds eaten by *Cydia*.

We multiplied quantities of food resources (seeds, flowers, flush, and caterpillars) by māmane tree density (number of trees per area) to determine the abundance of palila food resources per area of habitat.

Table 1.1. Average elevation, range of elevation, and number of stations sampled per month for phenology of individually marked māmane trees in eight study sites on and near Mauna Kea.

Study site	Average elevation (m)	Elevation range (m)	# Stations sampled per month (Mar 96–Jan 98)	# Stations sampled per month (Feb 98–Feb 99)	# Stations sampled per month (Mar 99–Dec 01)	# Stations sampled per month (Jan 02–Aug 02)
PL Makai	2700	2591–2804	55	31	31	31
PL Mauka	2440	2286–2591	51	25	25	25
Manao	2410	2286–2530	40	20	20	20
Ahumoa	2160	2073–2243	40	20	20	20
North	2330	2103–2560	30	30	0	0
South	2650	2463–2835	30	30	0	0
PFlats	2015	2006–2027	30	30	30	0
Kīpuka ʻAlalā	1805	1701–1911	30	30	0	0

Results

Forest Composition, Structure, and Recruitment

Forest composition and structure varied widely among study sites (Table 1.2). In forests supporting a viable breeding population of palila (PL Mauka and PL Makai), māmane was virtually the only tree species present. In adjacent forests, where fewer palila nested, māmane occurred equally (Manao) or secondarily (Ahumoa) to naio (Myoporum sandwicense). Māmane was relatively scarce at Kīpuka ʻAlalā, but it was the dominant tree species at the three other sites.

Table 1.2. Densities of trees (>2 m tall and wide) per hectare in sites presently and formerly occupied by palila. Only PL Mauka and PL Makai support a viable population of palila.

Site	Māmane	Naio	ʻĀheahea	ʻAʻaliʻi	Other	All
PL Mauka	116.1	–	–	–	0.1	116.2
PL Makai	70.8	0.7	–	–	–	70.8
Manao	45.8	43.0	9.5	–	18.4	116.7
Ahumoa	46.7	212.5	2.3	6.0	–	267.5
North	58.8	–	–	–	43.9	58.8
South	81.1	4.1	12.2	–	–	97.4
PFlats	81.8	41.5	3.8	3.8	33.4	151.0
Kīpuka ʻAlalā	14.8	304.1	–	92.7	20.1	445.0

Sapling densities varied over a wide range, but māmane saplings outnumbered naio everywhere except Kīpuka ʻAlalā and māmane saplings outnumbered even native shrub species at three sites (Table 1.3). Māmane recruitment also was high in adjacent forests at lower elevation on the western slope of Mauna Kea, although it was secondary to larger cohorts of ʻāheahea (*Chenopodium oahuense*) at Manao and ʻaʻaliʻi (*Dondonaea viscose*) at Ahumoa. Māmane was

Table 1.3. Densities of saplings (0.5–2 m tall and wide) per hectare in areas presently and formerly occupied by palila. Only PL Mauka and PL Makai support a viable population of palila.

Site	Māmane	Naio	ʻĀheahea	ʻAʻaliʻi	Other	All
PL Mauka	66.8	0.1	0.1	–	–	67.0
PL Makai	19.4	–	0.2	0.03	0.07	19.7
Manao	34.2	2.5	137.9	4.0	2.7	181.3
Ahumoa	75.8	7.9	24.4	83.9	3.7	195.7
North	34.5	–	–	0.6	20.1	55.2
South	39.1	–	82.0	–	–	121.1
PFlats	40.1	2.2	71.0	2.2	6.4	129.0
Kīpuka ʻAlalā	1.3	89.4	–	58.3	13.5	155.4

the principal sapling at only one potential reintroduction site (North). Although māmane comprised a substantial proportion of young trees at the South and PFlats sites, it was much less common than ʻāheahea. Māmane recruitment was nearly absent at Kīpuka ʻAlalā, where naio and ʻaʻaliʻi dominated the sapling population.

Availability of Māmane Food Resources

Annual production of māmane flowers was least distinct and regular at the West site (PL Mauka, PL Makai, Manao, and Ahumoa combined), where the elevation gradient was greatest (Figure 1.1). At Kīpuka ʻAlalā and PFlats, where the elevation gradients were small, flowering was more seasonal. Māmane pod production typically mirrored flowering patterns but tended to be offset by three to five months (Figure 1.2). The rainfall gradient at PFlats (Figure 1.3) may have diffused temporal patterns of flowering to some degree, but this effect may have been diminished by the drought during 1998–2000.

One of the most important measures of palila food resource availability is the number of pods per tree, which is probably most influenced by tree size. Trees on the western slope (PL Mauka, PL Makai, and Manao) produced large numbers of pods (Table 1.4). South and North site trees produced intermediate numbers of pods.

The availability of pods in different habitats is strongly influenced by tree density. The mean number of pods per hectare was high at two adjacent sites (PL Mauka and PL Makai) on the western slope (Table 1.5), where palila concentrate much of their nesting and foraging. Pod availability was low at Kīpuka ʻAlalā and intermediate elsewhere.

In addition to the number of pods per hectare, food availability also is affected by the average number of seeds produced per pod in different areas. For example, if pods in some areas typically produce twice as many seeds as elsewhere, the number of pods per hectare will not accurately reflect food resource availability. We found, however, that the number of seeds per pod did not differ greatly (range = 2.86–3.40) among our study sites (Table 1.6). Nevertheless, more seeds per pod were produced at PL Mauka and PL Makai, possibly indicating an effect of tree size.

The abundance of *Cydia* caterpillars found within māmane pods generally peaked in late summer on the western slope of Mauna Kea (Brenner *et al.* 2002). Similar to the abundance of māmane pods, *Cydia* abundance generally was greater at PL Makai and PL Mauka compared to

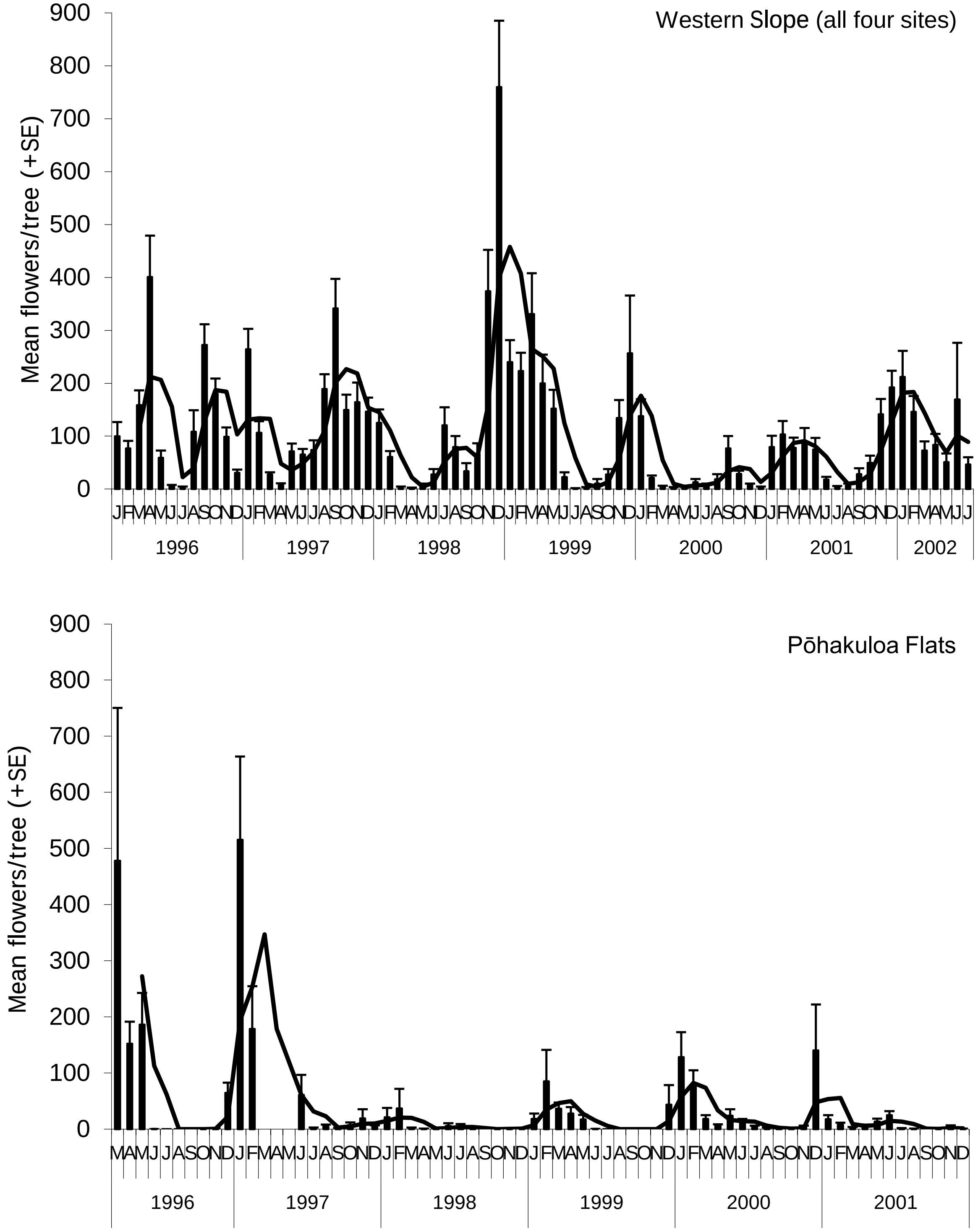
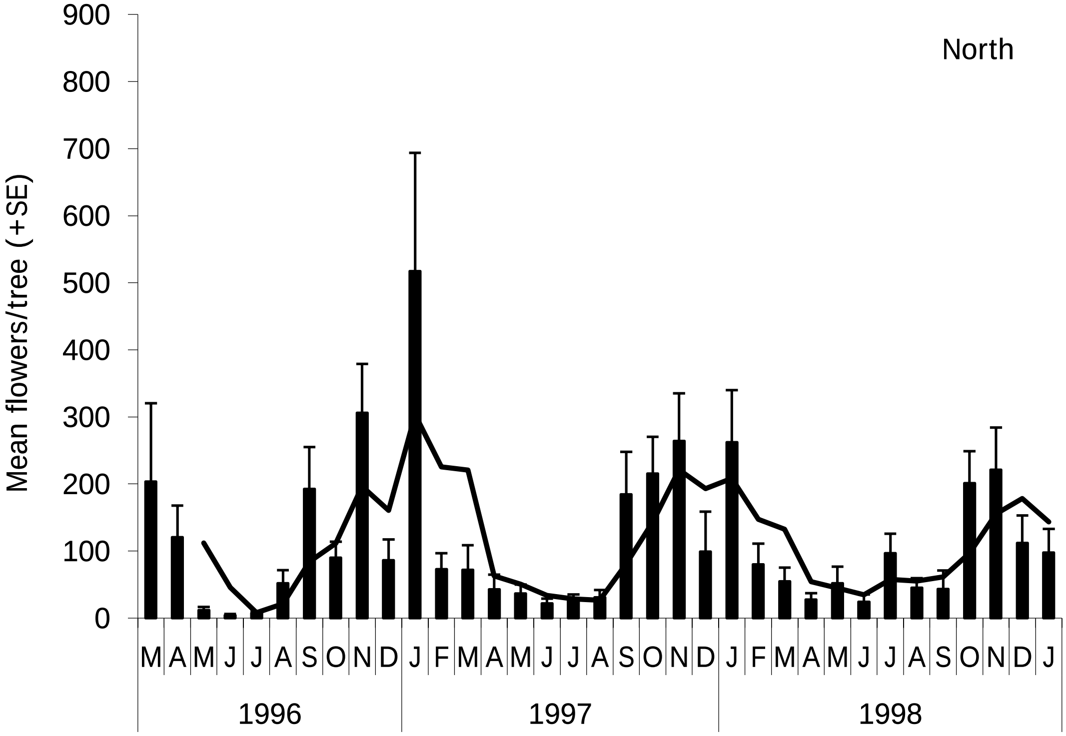


Figure 1.1a. Māmane flower production (monthly average [bars], standard error (SE), and three-period moving average [line]) at sites on the western slope of Mauna Kea and at Pōhakuloa Flats, Hawai‘i. The moving average illustrates the status of resources in the present and recent past to provide an alternative perspective of resource availability over time. Note that data were collected through July 2002 at West, December 2001 at Pōhakuloa Flats, and January 1999 at North and Kīpuka ‘Alalā.



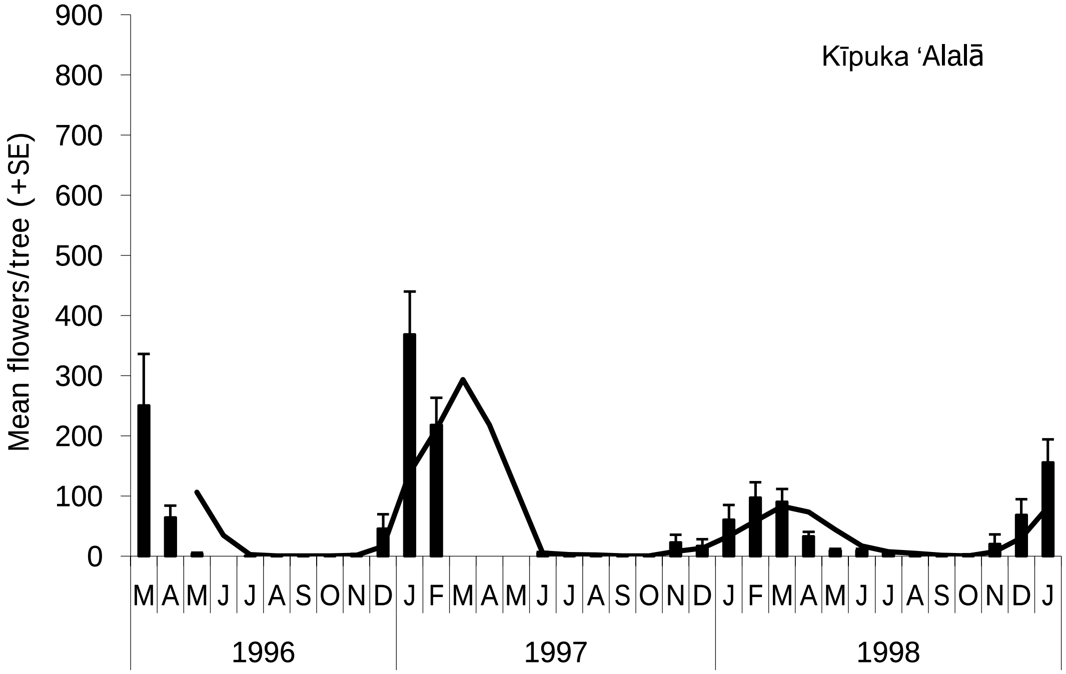
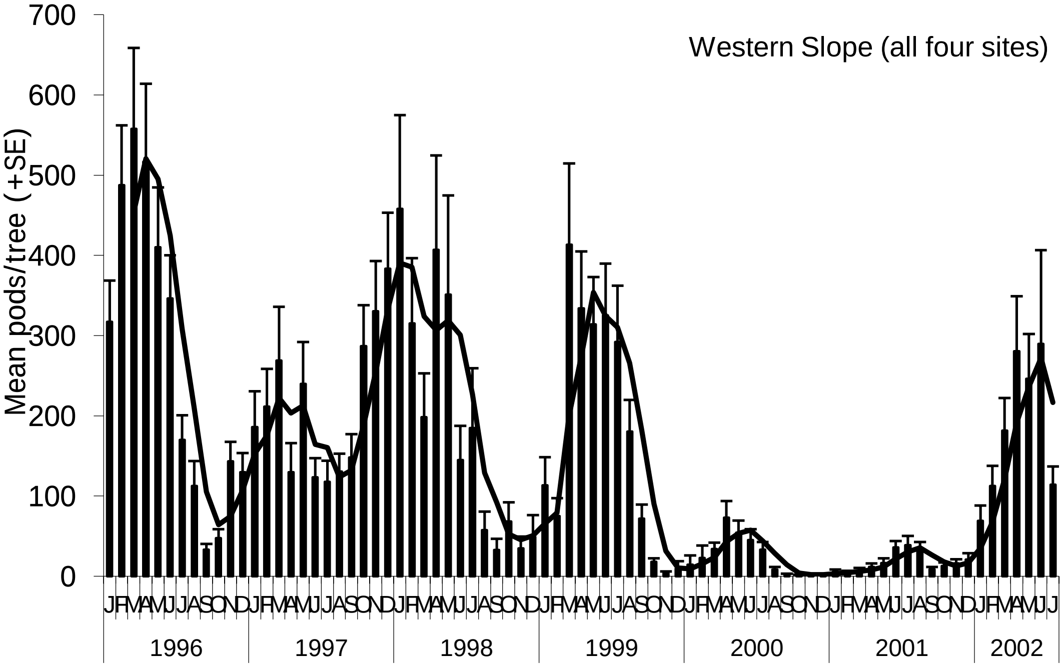


Figure 1.1b. Māmane flower production (monthly average [bars], standard error (SE), and three-period moving average [line]) at the North site of Mauna Kea and at Kīpuka ʻAlalā on Mauna Loa, Hawaiʻi. The moving average illustrates the status of resources in the present and recent past to provide an alternative perspective of resource availability over time. Note that data were collected through July 2002 at West, December 2001 at Pōhakuloa Flats, and January 1999 at North and Kīpuka ʻAlalā.



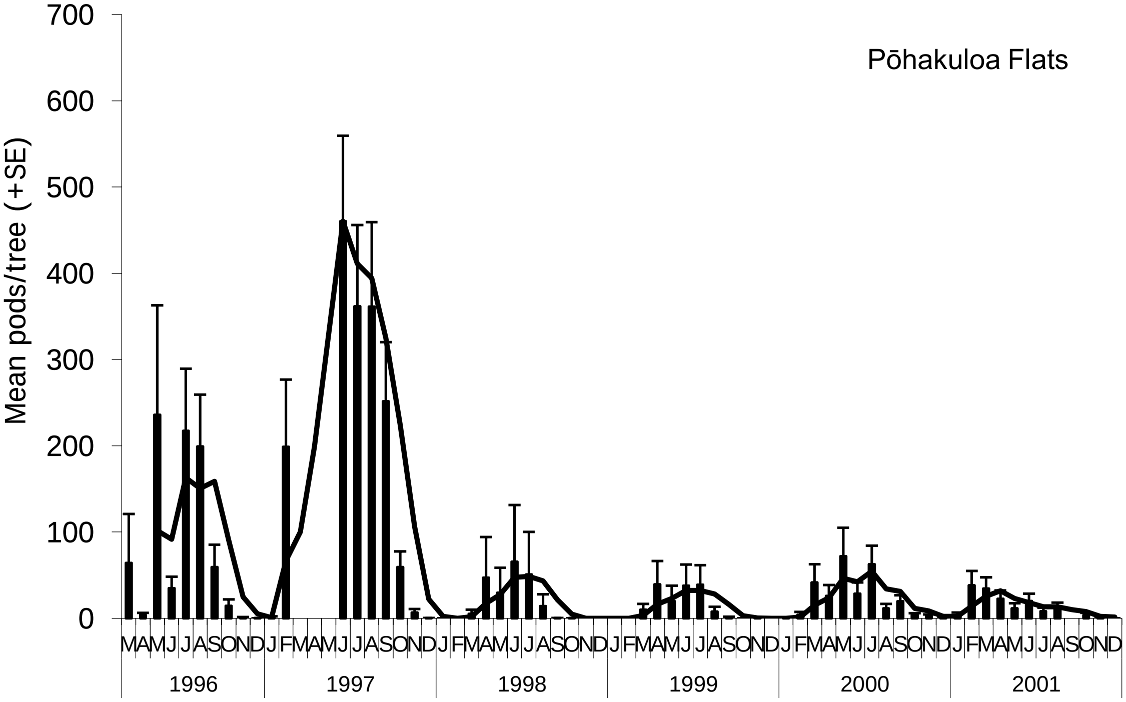
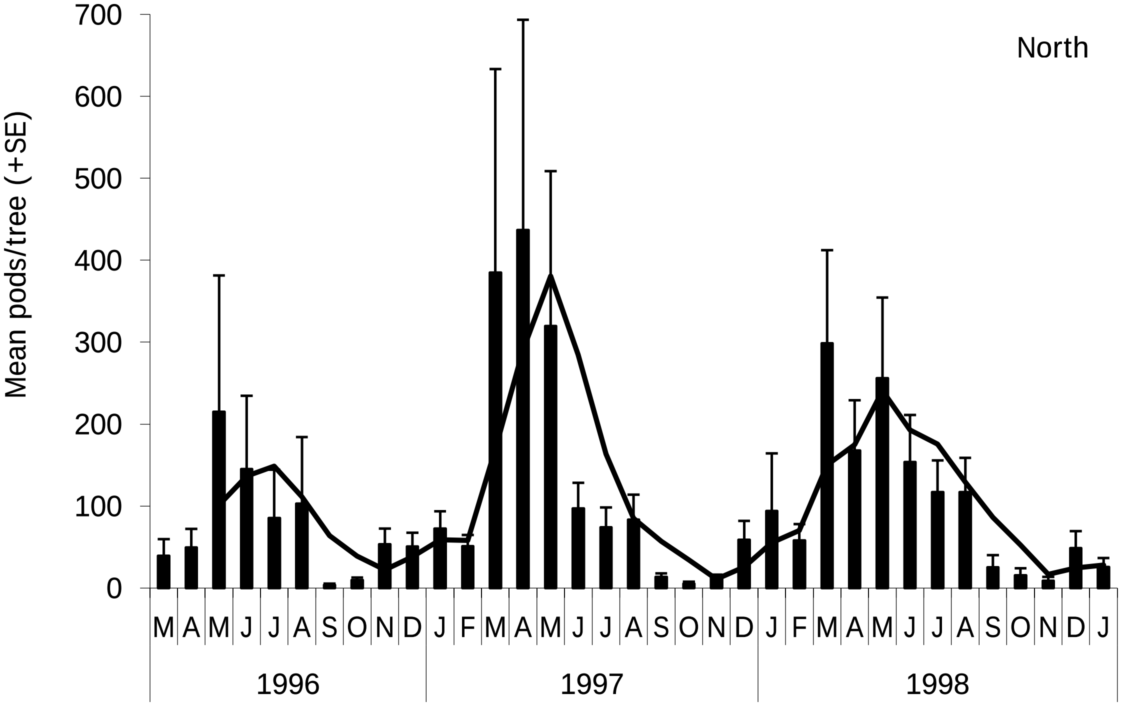


Figure 1.2a. Māmane pod production (monthly average [bars], standard error (SE), and three-period moving average [line]) at sites on the western slope of Mauna Kea and at Pōhakuloa Flats, Hawai‘i. The moving average illustrates the status of resources in the present and recent past to provide an alternative perspective of resource availability over time. Note that data were collected through July 2002 at West, December 2001 at Pōhakuloa Flats, and January 1999 at North and Kīpuka ‘Alalā.



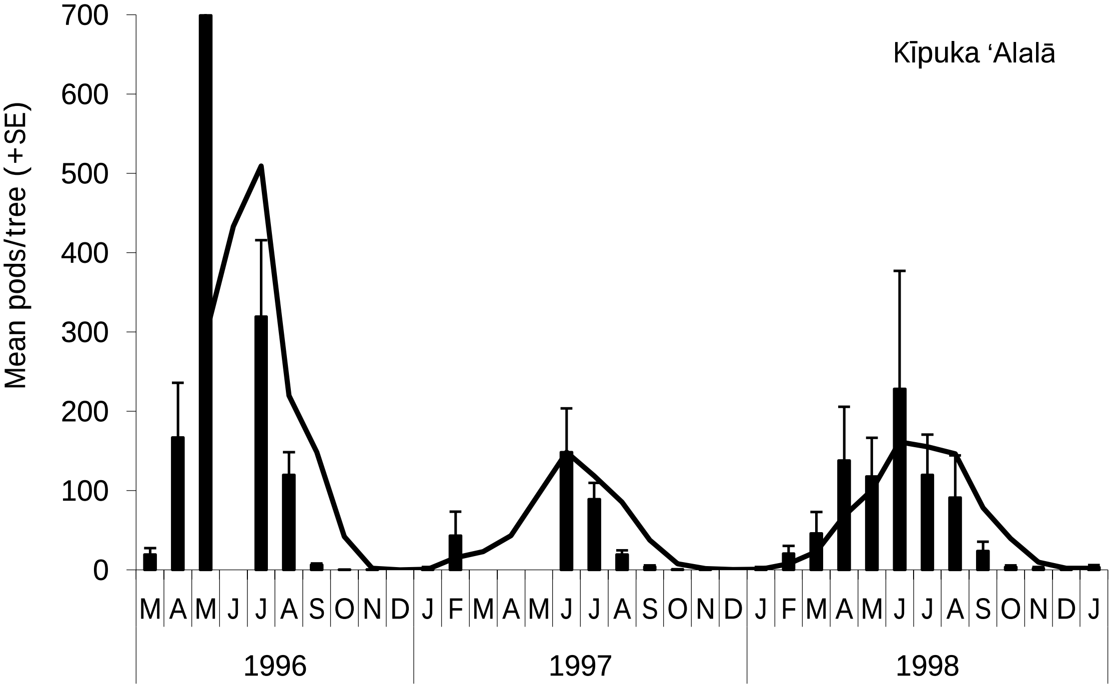


Figure 1.2b. Māmane pod production (monthly average [bars], standard error (SE), and three-period moving average [line]) at the North site of Mauna Kea and at Kīpuka ʻAlalā on Mauna Loa, Hawaiʻi. The moving average illustrates the status of resources in the present and recent past to provide an alternative perspective of resource availability over time. Note that data were collected through July 2002 at West, December 2001 at Pōhakuloa Flats, and January 1999 at North and Kīpuka ʻAlalā.

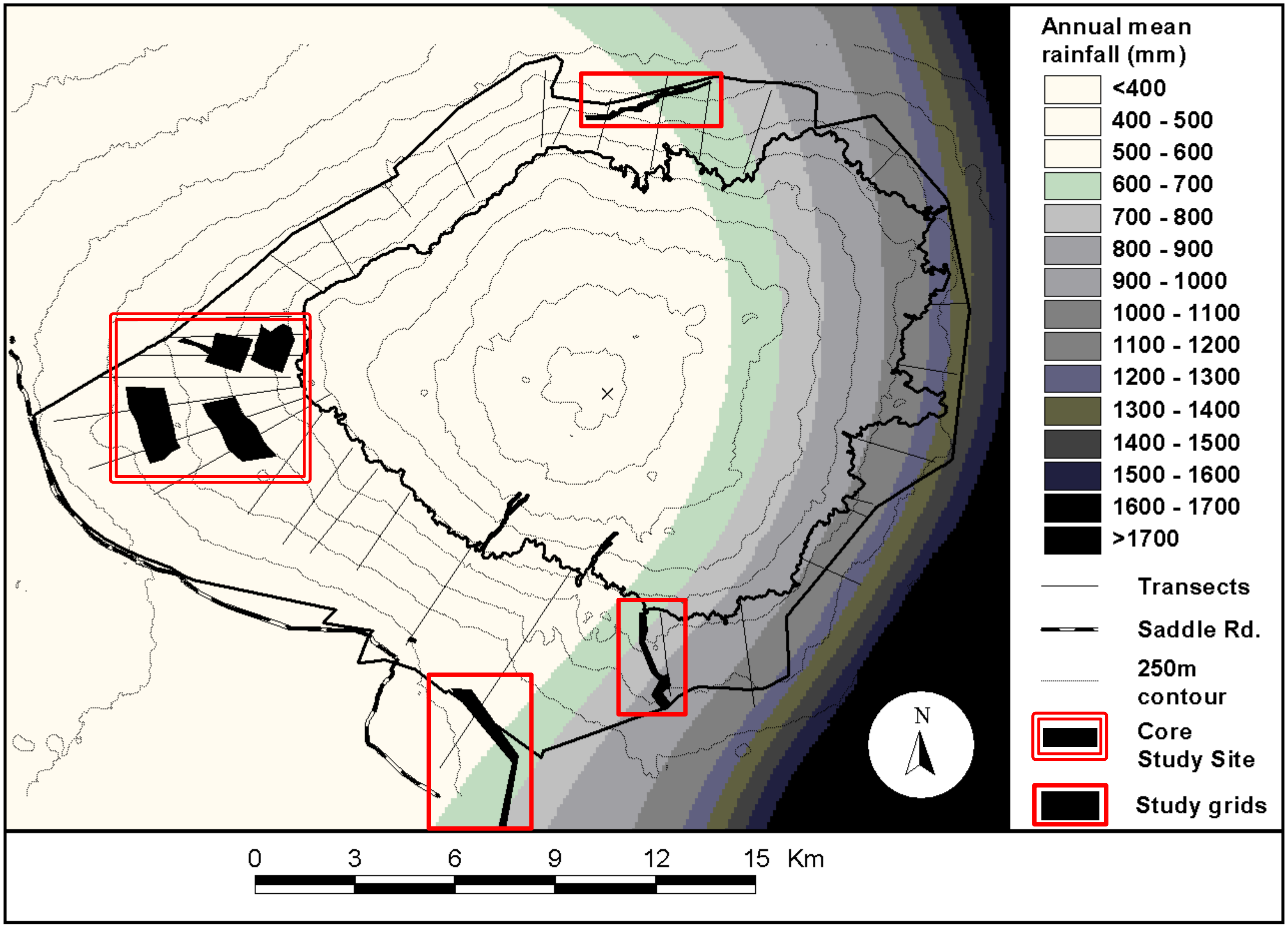


Figure 1.3. Mean annual rainfall isohyets (mm) for the seven study grids on Mauna Kea, including the four that compose the core study area on the western slope (adapted from Giambelluca *et al.* 1986). Kīpuka ʻAlalā is not shown.

Table 1.4. Summary statistics (mean, standard deviation [SD], standard error [SE], and sample size [*n*]) for the average number of pods per tree per month in eight study sites on and near Mauna Kea during March 1996–August 2001. Data collected only through February 1999 are indicated by [*], while data collected through December 2001 are indicated by [†].

Site	Pods/tree	SD	SE	*n*
PL Mauka	287.16	409.39	17.40	2581
PL Makai	173.48	399.98	10.00	2969
PL Mauka and PL Makai combined	226.35	724.73	9.73	5550
Manao	135.34	400.70	11.48	1902
Ahumoa	73.51	320.95	78.80	1946
North*	107.20	471.24	14.54	1050
South*	124.21	448.82	13.86	1049
PFlats†	52.72	218.00	5.08	1844
Kīpuka ‘Alalā*	76.63	516.77	16.89	936

Table 1.5. Summary statistics (mean, and sample size [*n*]) for the number of pods per hectare (ha) in eight study sites on and near Mauna Kea during March 1996–August 2001. Data collected only through February 1999 are indicated by [*], while data collected through December 2001 are indicated by [†].

Site	Pods/ha	*n*
PL Mauka	33,339.28	2581
PL Makai	12,282.38	2969
PL Mauka and PL Makai combined	21,152.41	5550
Manao	6198.57	1902
Ahumoa	3432.92	1946
North*	6303.36	1050
South*	10,073.43	1049
PFlats†	4312.50	1844
Kīpuka ‘Alalā*	1134.12	936

Table 1.6. Summary statistics (mean, standard deviation [SD], standard error [SE], and sample size [*n*]) for the number of seeds per pod in eight study sites on Mauna Kea during March 1996–August 2001. Data collected only through February 1999 are indicated by [*], while data collected through December 2001 are indicated by [†].

Site	Seeds/pod	SD	SE	*n*
PL Mauka	3.45	1.83	0.03	4301
PL Makai	3.38	1.80	0.03	4671
PL Mauka and PL Makai combined	3.41	1.82	0.02	8972
Manao	2.89	1.72	0.04	2444
Ahumoa	2.93	1.74	0.04	1953
North*	2.90	1.65	0.04	1754
South*	2.95	1.70	0.04	1694
PFlats†	2.86	1.67	0.04	1851
Kīpuka ‘Alalā*	2.86	1.75	0.05	1152

Ahumoa and Manao. Although fluctuations in abundance were common, *Cydia* were present, if only at low levels, on the western slope throughout the year. In contrast, peaks and declines of caterpillar abundance were more pronounced at the North site and at PFlats/South, where abundances typically increased three-to-four-fold for one-to-two months a year. *Cydia* abundance was the lowest at Kīpuka ʻAlalā, where caterpillars were absent from māmane pods several months each year.

The percentage of seeds eaten by *Cydia* caterpillars mirrors their abundance over time in the different study areas. On the western slope, 5–45% of seeds typically were consumed by caterpillars each month. Levels of seed predation exhibited multiple peaks per year and were most pronounced at PL Makai and PL Mauka. We observed moderate levels of seed predation at North and PFlats/South sites for two to three months per year. Similar to caterpillar abundance, seed predation at Kīpuka ʻAlalā was low due to the low number of *Cydia* in the area.

The estimation of *Cydia* availability based on local tree density revealed that PL Mauka and PL Makai sites contained the most caterpillars per hectare (Table 1.7). The South and North sites also supported relatively high densities of caterpillars. Mean number of *Cydia* per hectare was similar at Ahumoa, Manao, and PFlats. As with pod availability, Kīpuka ʻAlalā contained few caterpillar resources, which reflects both the low density of māmane trees in this area and the relative absence of *Cydia* for many months of each year.

Table 1.7. Summary statistics (mean and sample size [*n*]) for the number of *Cydia* caterpillars per hectare (ha) each month in eight study sites on Mauna Kea during March 1996–August 2001. Data collected only through February 1999 are indicated by [*], while data collected through December 2001 are indicated by [†].

Site	Caterpillars/ha	*n*
PL Mauka	6101.09	78
PL Makai	2788.10	77
PL Mauka and PL Makai combined	4349.76	155
Manao	495.89	72
Ahumoa	329.56	63
North*	1096.08	35
South*	1888.77	35
PFlats†	133.69	59
Kīpuka ʻAlalā*	34.46	32

Pod availability per unit area during the early portion of the breeding season (March through May), when palila nesting effort might be most affected (Lindsey *et al*. 1995), tended to be high in the West site (all four western sites averaged) relative to the three potential reintroduction sites (North, Kīpuka ʻAlalā, and PFlats/South; Figure 1.4). Again, pods were available at low levels at Kīpuka ʻAlalā.

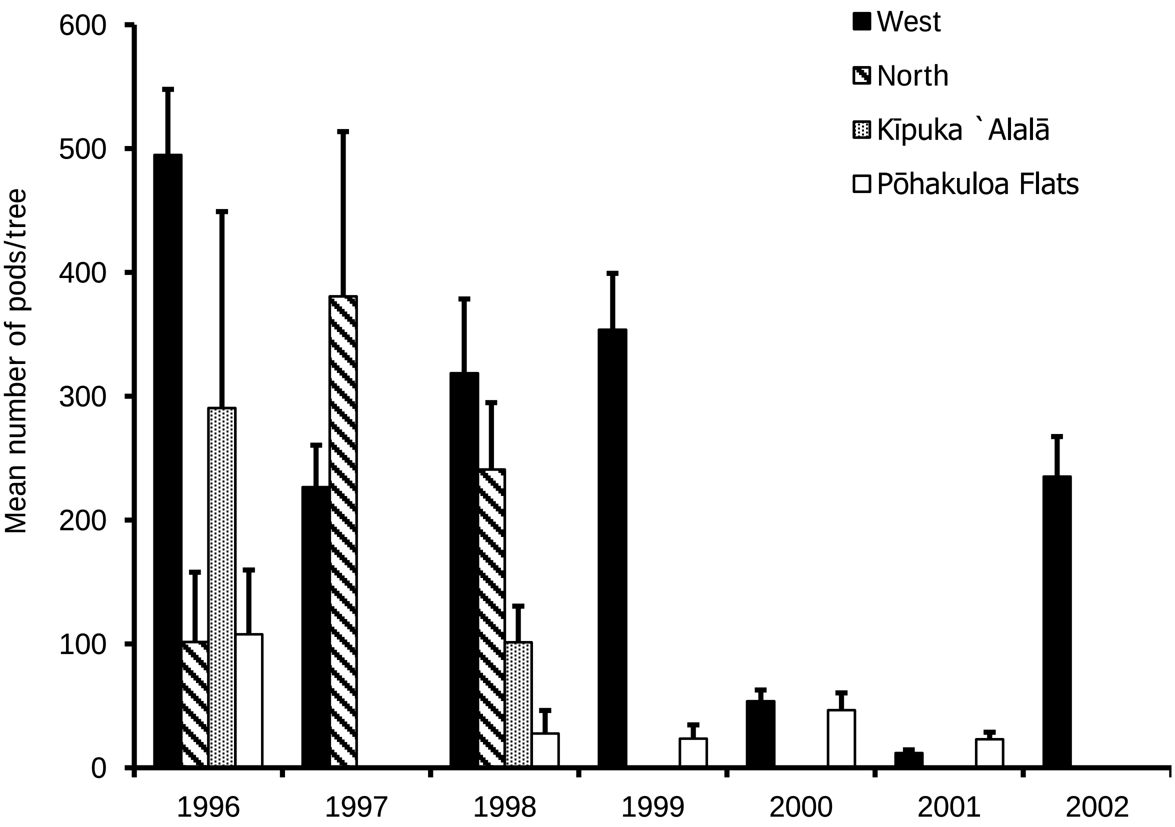


Figure 1.4. Māmane pod abundance per tree (mean and standard error) in the early portion of the palila breeding season (March–May) during 1996–2002.

Discussion

Forest Composition, Structure, and Recruitment

The density of māmane trees and saplings and the number of major woody species varied considerably among sites. At the two sites (PL Mauka and PL Makai) where palila concentrated their nesting and foraging activity, māmane was not only the most abundant tree species, it was virtually the only species. In adjacent areas (Manao and Ahumoa), where palila were less abundant, māmane was co-dominant or secondary to naio. Expanding the palila population would seem to depend mainly on increasing the density of māmane throughout the birds' range. Of the four sites considered for immediate reintroduction, South and North seemed most suitable in terms of māmane tree density. Trends in recruitment of young trees indicate that māmane will continue to dominate forests presently occupied by breeding palila (PL Mauka, PL Makai). Māmane recruitment was also high in adjacent forests on the western slope of Mauna Kea, although cohorts of ʻāheahea (Manao) and ʻaʻaliʻi (Ahumoa) were larger. Māmane was the principal sapling species at only one reintroduction site (North). Although māmane sapling density was at least as high at South and PFlats sites, ʻāheahea saplings were even more abundant. Māmane saplings were nearly absent at Kīpuka ʻAlalā, where naio and ʻaʻaliʻi dominated the sapling population.

Fire poses a major threat to palila habitat where alien grass cover is dense, particularly in PL Makai (Hess *et al.* 1999). However, even where grass cover was not dense, woody fuels (e.g., ʻāheahea, ʻaʻaliʻi, naio) have accumulated and the potential for fire was substantial. The rank order of sites with respect to woody growth was (high to low): Kīpuka ʻAlalā, Ahumoa, Manao, PFlats, South, PL Mauka, North, and PL Makai. The fire hazard was reduced at higher elevations (e.g., PL Mauka) due to lower densities of grasses and woody fuels. Nevertheless, a large fire within PL Mauka or PL Makai could jeopardize the core palila population and hamper the species' expansion into adjacent areas.

In three of the four sites considered for palila reintroduction, the potential for fire seemed high due to the accumulation of woody fuels and, in the lower elevations, alien grasses. Fire hazards seemed relatively low only at North due to generally low grass density, relatively low accumulation of woody growth, and somewhat moister conditions. At Kīpuka ʻAlalā, where māmane regeneration was severely reduced by browsing, there was much accumulated woody growth, principally naio and ʻaʻaliʻi, which could likely support large, destructive fires. In Mauna Kea Forest Reserve, where ungulate populations were culled on a regular basis, māmane regeneration was notable but variable, perhaps influenced by the density of alien grasses and numbers of remaining browsing animals. Herds and fresh evidence of sheep (*Ovis aries*) and mouflon (*O. gmelin musimon*) were observed in all areas but were most frequently observed in PFlats, Ahumoa, and Manao. Twigs of māmane trees were frequently damaged or removed by browsing, and bark was often stripped from saplings. Naio bark also was stripped, but branch tips were not browsed and recruitment did not seem affected (Hess *et al.* 1999).

Availability of Māmane Food Resources

The striking contrast in temporal patterns of māmane flower and pod production and *Cydia* caterpillar abundance between Kīpuka ʻAlalā and sites on Mauna Kea demonstrates the importance of an elevation gradient to the year-round availability of food resources for palila (Banko *et al.* 2002). Flowering and pod production were strongly linked to time of year. In areas where the forest extends along a large gradient of elevation, the production of flowers and pods occurred at high or peak levels over a long period of time. In contrast, in areas where there was only a small elevation gradient, such as Kīpuka ʻAlalā, flowers and pods were produced in greater synchrony, resulting in little or no food available for palila during several months of the year. The rainfall gradient evident across PFlats may not have significantly extended the duration of māmane flower and pod production due to prolonged drought.

The abundance of *Cydia* caterpillars was related to māmane pod production (Banko *et al.* 2002). In sites on Mauna Kea, *Cydia* occurred at moderate levels year-round, peaking at least two times per year, depending on the specific area. In contrast, *Cydia* abundance at Kīpuka ʻAlalā was low or nonexistent throughout a three-year period. Our decision to discontinue monitoring phenology at Kīpuka ʻAlalā was based on the predictable and distinct pattern of annual peaks in flower and pod production and low numbers of caterpillars.

Although the average abundance of pods per tree and caterpillars per pod indicate the quality of palila habitat, tree size and density greatly influenced this estimate. Thus, a more useful index of habitat quality is an estimate of the number of pods or *Cydia* caterpillars per unit area. Using this measure, we found that the western slope of Mauna Kea offered much greater availability of māmane pods to palila than other areas. Similarly, we found that two western study sites, PL Mauka and PL Makai, supported the greatest abundance of *Cydia* caterpillars.

This underscores the need for increased forest regeneration across the entire range of Palila Critical Habitat, especially in areas where palila may be reintroduced.

Evaluation of Reintroduction Sites

Many important factors were considered in selecting the reintroduction site:

- *Size of existing and potentially recoverable māmane forest*. A large tract of forest is required to support a population of palila; large forest areas are needed by palila in order to locate and exploit locally favorable foraging opportunities.

- *Presence of elevation or rainfall gradients that extend the temporal distribution of māmane food resources*. Timing of peak flower and pod production generally varies with elevation and rainfall, and birds may move several kilometers to exploit locally abundant resources.

- *Density of māmane trees*. Tree density, which reflects the long-term history of browsing by ungulates, contributes greatly to the availability of seeds and other foods required by palila.

- *Density of māmane saplings*. Sapling density, which reflects the short-term history of browsing by ungulates, foreshadows the future composition of the forest.

- *Availability of māmane seeds*. Seed availability is a function of tree density, tree productivity, and number of seeds per pod; annual tree productivity is influenced by rainfall and is highly variable.

- *Availability of Cydia*. *Cydia* caterpillar availability is a function of tree density, tree productivity, number of seeds per pod, and parasitism by wasps; annual tree productivity is highly variable, and it strongly affects annual *Cydia* availability within an area.

- *Ungulates*. Browsing ungulates are incompatible with palila restoration because they alter montane and subalpine forest structure and composition and greatly limit māmane survival, regeneration, and productivity.

- *Fire*. Fire threatens the dry forests of Mauna Kea and of the inter-mountain plateau; palila populations probably will crash if large areas of habitat burn and become unusable to birds for more than a year.

- *Food competitors*. Palila require māmane trees for most of their food (flowers, seeds, young pods, new leaves, *Cydia* and other caterpillars), making them highly vulnerable to competitors, especially when māmane resources are reduced due to drought. Although *Cydia* caterpillars also consume māmane seeds, they are valuable foods of palila, especially nestlings; nevertheless, caterpillar parasites, ants, yellowjackets, and other alien pests can reduce food availability and adversely affect palila survival and breeding success.

- *Predators*. In māmane-dominated forests, rats (*Rattus rattus*) do not seem to limit palila numbers or nesting success; but, rats may more seriously threaten palila where naio, a preferred resource of rats, is common. Reducing rats in naio forests may allow palila to nest and survive in greater numbers. Cats (*Felis catus*) and owls also prey on palila.

- *Human disturbance*. Although palila seem fairly tolerant of limited human disturbance, they may be vulnerable to more intense or prolonged disturbance from firearms, low-flying aircraft, vehicles, and military activity.

- *Disease*. Avian malaria and pox seem not to be a serious threat within the present range of palila due to the low prevalence of mosquitoes.

The time scale for reintroduction affected the ranking of release sites. The size and structure of the forest and especially the range of elevation over which māmane was distributed were important short-term considerations for palila reintroduction sites, but even highly degraded habitats can be restored over time (Banko *et al.* 2009). Where habitat structure was similar among areas, the mix of environmental assets and liabilities was key to selecting a site (Table 1.8). Distance from and connectivity with the source population was also considered to be an important factor in reducing the impacts of catastrophic events (e.g., fire, hurricane) and environmental perturbations (e.g., drought, epidemics), yet allowing occasional genetic influx.

Table 1.8. Assets and liabilities of four sites considered for palila reintroduction (1996–2002).

	North	South	PFlats	Kīpuka ʻAlalā
ASSETS				
Size of forest tract	Restricted; can be enlarged	Large with PFlats available	Large with South available	Restricted; little chance for expansion
Elevation or rainfall gradient	Elevation & possibly moderate rainfall	Elevation & possibly moderate rainfall	Rainfall	None
Māmane tree density	Moderate	Moderate-high	Moderate-high	Very low
Māmane sapling density	Moderate	Moderate	Moderate	Very low
Predicted annual availability of māmane seeds	Moderate-low	Moderate	Moderate	Very low
Predicted annual availability of *Cydia*	Moderate	Moderate	Very low	Very low
LIABILITIES				
Ungulates	Low-moderate	Low-moderate	Low-moderate	Very high
Fire	Low-moderate	Moderate-high	High-moderate	Moderate-high
Food competitors	Moderate-high	Moderate-high	Very high	Very high
Predators	Moderate	Moderate	High?	High?
Human disturbance	Low	Moderate	Very high	Very high
Disease	Low?	Low?	Low?	Unknown

Kīpuka ʻAlalā

When assets and liabilities were qualitatively compared, Kīpuka ʻAlalā scored very poorly because it had many liabilities and its biological assets were not outstanding (Table 1.8). However, the most serious liability at Kīpuka ʻAlalā, the presence of large numbers of sheep and goats (*Capra hircus*), has been remedied by fencing the area and removing the animals. After a few decades, the māmane forest might recover sufficiently to sustain a small to moderate number of palila. If māmane density returns to its full potential, food availability will be greatly enhanced. Nevertheless, Kīpuka ʻAlalā has little or no elevation or rainfall gradient, and it is a relatively small area, isolated from other māmane forests where palila might temporarily take refuge when local conditions become marginal. Nevertheless, plans are moving forward to manage māmane forests on adjacent privately-owned lands, which could supplement habitat in Kīpuka ʻAlalā. Even with habitat recovery, the threat of fire from military training and other causes may undermine palila reintroduction.

The conspicuous presence of food competitors (see Chapters 19–23), most notably parasitoid wasps that attack *Cydia* caterpillars but also including predacious ants and yellowjacket wasps (*Vespula pensylvanica*), presents another challenge to reestablishing palila in Kīpuka ʻAlalā. Rats also may be a threat in Kīpuka ʻAlalā due to the huge cohort of naio that can provide a nearly continuous supply of fruit when rainfall is adequate. Control of rats and other predators should be relatively feasible by the time other habitat liabilities are overcome.

North

The North site offered a favorable ratio of biological assets to liabilities. Because populations of browsing ungulates have been culled, māmane recruitment was relatively high. Although māmane seed availability was moderate during the study period, increasing tree density and tree size should result in greater food availability over time. The recovering māmane forest on the ʻaʻā lava flow below Puʻu Mali on lands that were recently included within Mauna Kea Forest Reserve broadens the gradient of elevation and increases the area available for habitat restoration. As a result, opportunities for palila to find food during the year should increase as the forest is restored.

The North site receives the most precipitation of the four sites being considered for palila reintroduction; therefore, the threat of fire is expected to be less, especially because the site is relatively remote and there is comparatively little human disturbance in the area. Nevertheless, fire ignited by lightning burned 162 ha of pastureland below the North site in August–September 2006 (Department of Land and Natural Resources 2006). The most serious liability at the North site, where *Cydia* caterpillars were abundant, may be the relatively high incidence of parasitism on the caterpillars. Yellowjacket wasps could also present potential management challenges. Controlling rats, cats, and other predators should be feasible.

South

The South site also featured more assets than liabilities when considering palila reintroduction. Of particular importance was the large size of the forest. Although truncated by cattle pastures at lower elevations on the southeastern flank, the forest is contiguous with PFlats to the southwest. Except for the large fire that burned much of PFlats in 2010 (Department of Land and Natural Resources 2010), the two areas together would have provided the largest area of forest on Mauna Kea in which to reintroduce palila. We characterized the South site as having moderately high levels of woody fuels, and it was fortunate that the 2010 fire in PFlats was contained before burning upslope.

Māmane tree densities at the South site were similar to those in nesting areas on the western slope. Māmane sapling density was intermediate, indicating that foraging conditions for palila could continue to improve. *Cydia* caterpillars at the South site were as numerous in pods as they were at the PL Mauka and North sites (Brenner *et al.* 2002; see Chapter 19: Threats to Food Resources: *Cydia* Caterpillar Parasitism). Moreover, caterpillar parasitism rates were lower than they were at all sites except PL Mauka and PL Makai. Disturbance from activities at Pōhakuloa Training Area is another factor that could possibly impede palila restoration efforts in the future.

Pōhakuloa Flats

Before a 561 ha fire in 2010 (Department of Land and Natural Resources 2010), PFlats and the contiguous South site together constituted a large forest tract that was biologically suitable for reintroducing and maintaining a palila population. By itself, PFlats is relatively limited in size; nevertheless, it is situated along a rainfall gradient which runs from east to west and which extends the temporal availability of māmane seeds and other palila foods. Māmane tree density was moderately high, and māmane saplings were moderately abundant before the fire.

Despite the relative abundance of māmane trees, PFlats produced very few *Cydia* caterpillars. Caterpillar parasitism in PFlats was virtually 100%, much higher than the rate in the forests above (South site), and ants and yellowjackets were relatively common. Even before the fire that burned much of PFlats, controlling food competitors would have posed a challenge to reestablishing a breeding population of palila in the area. In addition, naio density was relatively high before the fire and may have supported large numbers of rats and possibly cats. The accumulation of woody growth of naio and other trees and shrubs also supported the fire that burned much of the habitat. A potential challenge to reintroducing palila in PFlats even after it recovers from the fire would be the disturbance of military training. The proposed realignment of Saddle Road also could affect efforts to restore palila to the area.

In summary, when the four candidate sites were evaluated individually for their suitability for reintroducing palila in the near-term, North and South sites exhibited the most potential, PFlats demonstrated moderate potential, and Kīpuka ʻAlalā had low potential. Before the 2010 fire in PFlats, the South and PFlats sites together were second only to the western slope of Mauna Kea in size and quality of suitable forest. In this combined region, the phenology of māmane pod production would be influenced by both an elevation gradient (South) and a rainfall gradient (PFlats) that might increase the temporal availability of food to palila. The potential for reintroducing and maintaining a second population of palila on the southern slope would be additionally improved by restoring māmane forest on the pasturelands to the east of PFlats. Forest restoration at lower elevations would provide palila enhanced access to food resources and a larger area of habitat. Nevertheless, in the face of continued human activity in PFlats and cattle grazing to the east, the next best area for palila reintroduction is the North site. Here cattle grazing has been eliminated below Mauna Kea Forest Reserve in order to enhance the size and carrying capacity of the forest. In Kīpuka ʻAlalā, where ungulates have also been eliminated, the habitat will require decades of recovery before palila can be reintroduced.

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2 TRANSLOCATING WILD PALILA

Paul C. Banko, Chris Farmer, Kevin W. Brinck, Luanne Johnson

Introduction

Palila (*Loxioides bailleui*) are in danger of extinction largely because they are concentrated on the western slope of Mauna Kea (van Riper *et al.* 1978; Scott *et al.* 1984; Jacobi *et al.* 1996; Banko *et al.* 1998; Gray *et al.* 1999; Leonard 2008; Banko *et al.* 2009, 2013; Camp and Banko 2012). In order to reduce their vulnerability to local catastrophes, the U.S. Fish and Wildlife Service (2006) recovery plan requires the creation of additional viable populations elsewhere on Mauna Kea and throughout their historic range. Because palila do not seem to quickly resettle areas of recovering māmane (*Sophora chrysophylla*) forest on their own, our goal was to determine the efficacy of two reintroduction methods: translocation of wild birds and release of captive-reared birds. We conducted translocation trials in which wild palila were moved from the western slope to the northern slope. In partnership, the Zoological Society of San Diego developed techniques for captive propagation at the Keauhou Bird Conservation Center, and they released some of these birds on the northern slope of Mauna Kea (see Chapter 4: Release and Monitoring of Captive-reared Palila).

Palila were first translocated in March 1993, when 35 birds were moved from the western to the eastern slope of Mauna Kea in order to bolster the small population at Puʻu Kanakaleonui (Fancy *et al.* 1997). Fancy *et al.* (1997) found four nests of translocated birds, two of which fledged young. The survival of the fledglings was not determined. They also found that 40% (14/35) of their birds remained on the eastern slope after eight weeks, and that four palila died soon after their release on the eastern slope. No translocated birds have been seen near Puʻu Kanakaleonui since 1996, although surveys were conducted during annual point counts both on established transects and by sweep-searches of the entire area.

The initial results of the 1993 pilot project suggested that translocation could become a useful management tool if the persistence, survival, and breeding success of palila could be improved at the translocation site. Therefore, we sought to determine how long palila would persist in an area of their former range after being translocated there. In particular, we were interested in the tendencies of palila to disperse over an intermediate distance (16 km) between western (capture) and northern (release) sites, given that palila had been translocated nearly twice as far to the eastern slope in 1993 (Fancy *et al.* 1997). We also wanted to know how palila would respond to habitat conditions on the northern slope, which we deemed suitable but smaller in size and inferior in quality compared to their place of capture on the western slope (Banko *et al.* 2013; see Chapter 1: Evaluating Sites for Reintroduction). Another objective was to evaluate how age or sex might affect the persistence time of individuals in the translocation area. Many of the adult palila translocated by Fancy *et al.* (1997) emigrated within eight weeks; therefore, we initially translocated younger individuals for comparison. We also wanted to determine whether translocated birds would readily find mates and breed, especially given our constraints in moving more than a few birds per day and our limited knowledge of the breeding history of wild individuals. Therefore, we translocated primarily adult birds in later trials. We invested heavily in monitoring translocated birds to address these questions, to determine the success of translocated palila in producing offspring, and to evaluate their survival in the habitat conditions prevailing on the northern slope. Future publications will provide details about site assessment and selection; translocation procedures; effects of translocation on bird condition, health, and behavior; and recommendations for future reintroductions of palila.

We first identified sites where food would be adequate for sustaining a long-term reintroduction effort and where threats could be managed (see Chapter 1: Evaluating Sites for Restoration). The range of elevation over which habitat was distributed was a key criterion because the phenology of māmane varies with elevation and thus influences the availability of māmane pods and flowers during the year (Scott *et al.* 1984, Fancy *et al.* 1993, Lindsey *et al.* 1995, Banko *et al.* 2002a). Palila densities are positively correlated with the number of māmane pods at different elevations (Hess *et al.* 2001). Palila translocated to Pu'u Kanakaleonui in 1993 may have remained a short time because the forest on the eastern slope of Mauna Kea has been reduced to a narrow range of elevation. As a result, they may not have found sufficient food throughout the year.

After evaluating the suitability of four potential release sites, including two in Pōhakuloa Training Area, we determined that the northern slope of Mauna Kea was a relatively favorable site for palila based on the mix of environmental assets and liabilities (see Chapter 1: Evaluating Sites for Restoration). Habitat degradation by feral sheep (*Ovis aries*) and mouflon sheep (*O. gmelini musimon*) likely contributed to the extirpation of the palila population on the northern slope (Hess *et al.* 1999; see Chapter 5: Population Trends and Response to Environmental Factors), but populations of browsers have been somewhat reduced within Mauna Kea Forest Reserve since 1980, and portions of the māmane forest have recovered to some degree (Banko *et al.* 2013). Moreover, māmane and other native trees and shrubs are recovering on the 'a'ā lava flow that extends below the forest reserve near Pu'u Mali (see Chapter 26: Vegetation Surveys on Mitigation Parcels). Also in favor of the northern slope was its relative isolation from human disturbance and environmental perturbations that might affect birds on the western slope. Additionally, the vegetation between the northern and western slopes was sparse, potentially inhibiting the return of birds to the western slope and allowing a relatively discrete population to become established.

We suspected that the adult palila (34 of 35 palila were after-second-year birds) translocated in March 1993 might have returned quickly to the western slope because they had already established pair bonds and nesting territories or had developed strong affinities to their natal home ranges. We predicted that translocating younger birds that had not previously paired or nested would result in increased persistence at the release site. We also translocated birds at different times of the year to determine whether the annual cycle of the birds might influence the outcome. The birds from the 1993 translocation were held a median of 25.1 hours before translocation (Fancy *et al.* 1997). Based on simulated translocation trials involving surrogate species (Work *et al.* 1999), we predicted that transporting and releasing palila soon after capture would decrease stress and weight loss, thereby increasing short-term survival.

We also initiated a study of the birds' roosting behavior when we discovered that predators had killed some translocated palila during the night. Understanding characteristics of roosting habitats and the trees selected is important because birds spend nearly half their time at roost. A comprehensive study of roost site selection in bats (Vonhof and Barclay 1996) approached the problem in a systematic way and served as a model for this study. In addition, we adapted ideas from nest site selection studies (Matsuoka *et al.* 1997).

Methods

Study Area

The palila is found only in subalpine dry forest (Gagné and Cuddihy 1999) that encircles Mauna

Kea (summit 4,205 m) between 1,800 and 2,900 m elevation on the island of Hawaiʽi (19°53'N, 155°26'W; see Figure I.1). Although 244 km^2 of this area is designated as critical habitat (U.S. Fish and Wildlife Service 1977, 1986, 2006), over 95% of the palila population occurs within just 30 km^2 of habitat on the western slope (Banko *et al.* 2013). The forest on the western slope (i.e., the source or capture site for translocation) is dominated from 1,800 to 2,200 m elevation by māmane and naio (*Myoporum sandwicense*) and pure māmane from 2,200 m to tree line at 2,900 m (Hess *et al.* 1999). Native shrubs, grasses, and other forbs are scattered throughout the woodland, whereas alien grasses and other herbaceous cover are particularly dense at mid and low elevations (Banko *et al.* 2002a). The vegetation at the reintroduction area on the northern slope, located at least 16 km from the capture site on the western slope, is generally similar, but naio trees are much less abundant, native shrubs are more common, and large patches of black volcanic ash support little ground cover.

Subalpine dry forest on Mauna Kea usually lies above the trade wind inversion, resulting in a dry (511 mm annual rainfall) and cool (11°C average annual air temperature) but variable climate (Juvik *et al.* 1993). Wind direction reverses twice daily, relative humidity is often highest during daytime hours, and monthly rainfall may vary by two orders of magnitude. During droughts, which are frequent on Mauna Kea, cloud interception by vegetation can result in nearly 50% more precipitation falling through tree canopies to the ground (Juvik and Nullet 1993). However, air temperatures are relatively stable, varying more during the day than they do seasonally (Juvik *et al.* 1993).

Field Protocols and Data Analysis

Translocation

After initial development of techniques using surrogate species (Work *et al.* 1999), we translocated 188 birds during six episodes: February–March 1997 (T1), October 1997–March 1998 (T2), November–December 1998 (T3), April 2004 (T4), March–April 2005 (T5), and March–April 2006 (T6). Four birds were re-captured and translocated a second time in subsequent years, meaning 184 unique individual birds were moved. We changed the capture timing and intensity among translocations to test the effects of season, bird age, and concentration of birds moved on individual long-term persistence and reproduction. During the first three trials, young birds were targeted, but in the latter three trials, we focused on moving as many suitable birds as possible in a short time to establish a breeding population on the northern slope.

All birds were captured at eight different banding stations within the core population on the western slope, and 166 (88%) were captured at three stations within 3 km of each other. We arbitrarily designated birds for translocation to the northern slope or for release as controls at the capture site during T1−T4, but control birds were not deployed during T5 and T6. We moved birds of all age classes (Jeffrey *et al.* 1993), including hatch year (HY), after hatch year (AHY), second year (SY), after second year (ASY), and undetermined (U). Sex was determined at capture using Jeffrey *et al.* (1993), and DNA from feather pulp or blood was later analyzed (Patch-Highfill 2008) to verify or, in a few cases, change the sex designation. Birds were not moved if they did not meet our targeted age or sex criteria for that translocation or if they were in breeding condition, physiologically stressed, older than 10 years, or if a probable mate or offspring was calling nearby at the time of capture.

Transport in all translocations was by an air-conditioned, four-wheel-drive vehicle, but holding and transport protocols differed between the early translocation trials (T1–T3) and the later ones (T4–T6). In T1−T3, palila were housed in individual pet carriers that were lined with foam, provided with perches, and secured to a 140 x 29 x 2 cm board that was suspended by elastic cords to the sides of the vehicle to provide shock absorption while also being held steady by a passenger in the back seat. In the later translocations, palila were held in cages (28 x 20 x 20 cm, 1.3 cm rubber-coated wire mesh) that were similarly attached to a suspended and hand-steadied board (six cages per board). Vehicles left immediately in T1 and T2, but during T3 the birds were allowed to acclimatize to their cages for 15 minutes prior to transport. In the later translocations (T4–T6), single birds were held in the individual holding cages with two perches, and then the entire day's release group was transported to the northern slope in the early afternoon. Cages were covered with a cloth to keep the birds calm in semi-darkness, and the birds were caged in the shade near the banding stations. Weather conditions on the northern slope were determined before departing, and if there was inclement weather, then the birds were released at the capture site and no translocation occurred that day (*n* = 2 palila).

Bird health and behavior were regularly monitored at the capture site and during transport by staff trained in avian first aid. If a bird was agitated for more than 15 minutes, the vehicle was stopped to allow the bird to calm itself. If the bird did not perch calmly after the rest, it was returned and released at its capture site (*n* = 2 birds). During T1–T3, birds were provided with measured quantities of māmane pods and flowers in their carrier, and changes in food weight were recorded. During T4–T6, birds were provided with *ad lib* food, including apple (*Malus domestica*) slices, and native *Thyrocopa* sp. caterpillars were provided in T4. No water was provided because there is no surface water on Mauna Kea and palila obtain their water from food (Banko *et al.* 2002b).

We measured changes in weight and estimated the relative proportion of urates in the feces of birds to evaluate the degree to which palila were stressed by translocation. Birds were weighed immediately before their release and compared with their weight at capture (T1−T6) and before transport (T4−T6). Weight change among translocations was tested using a t-test, and linear regression was used to examine the effect of holding time on weight change. Any bird that lost 5% or more of its capture weight during T4−T6 was given a subcutaneous injection of 0.5 cc lactated Ringer's solution in the medial thigh (Quesenberry and Hillyer 1994). Birds were examined for any behavioral indications of stress or discomfort and treated until the condition was alleviated. Feces with <25% or >75% urates grossly indicated that birds were calorie deficient and presumably physiologically stressed (Work *et al.* 1999). During T1 and T2, we lined each transport carrier with paper, then counted and classified the fecal samples into three categories (<25%, 25–75%, and >75% urates). Field personnel were trained by Greg Massey (DVM, Hawaiʽi Department of Land and Natural Resources) and by experienced project staff to administer first aid to birds that were injured or highly stressed. Avian first-aid kits contained an oxygen tank, heat pads, lactated Ringer's solution, steroids, and tape for splints. We consulted with Dr. Massey by cellular telephone when questions or emergencies arose.

Although we supplied birds with food during transport, we did not provide supplemental food or hold birds in an aviary on the northern slope; therefore, we conducted a "hard" release. We released the translocated birds near the lower edge of the contiguous māmane forest near the bottom of transect 116 (Scott *et al.* 1986) above Puʽu Mali on northern Mauna Kea at approximately 2,100 m elevation (Figure I.3). Birds translocated during T1, T2, T4, and T6 were released close to the same māmane tree, which offered shelter and pods and flowers (when in season). During T3, two birds were released at the same site, but the other two were released in a grove of koa (*Acacia koa*) trees approximately 300 m upslope. Most T5 birds also were released at the primary location, but following the deaths of several palila in the vicinity of this site, the remaining birds were released 1.2 km west along the main forest reserve road to reduce the risk of predation.

Monitoring

All palila received a unique combination of three colored plastic bands, a numbered U.S. Geological Survey aluminum band, and 173 of 188 birds (92%) received radio-transmitters (Dougill *et al.* 2000). During T5 and T6 we did not have enough transmitters for every translocated bird, so 13 and 2 birds, respectively, were not radio-tagged. Monitoring effort varied greatly among translocations due to the availability of personnel and other logistical constraints. Intensive monitoring surveys occurred in two periods, February 1997–January 1999 and April 2004–August 2007. After August 2007, we shifted from intensive monitoring to two-to-four-day surveys that occurred two to four times annually through 2011 and once in early 2012. These periodic surveys totaled 989 person-hours of search effort and represented about 15% of the intensive monitoring effort, when we tracked or re-sighted the birds daily to weekly. Radio-tagged birds were usually tracked using handheld receivers and antennas, and we attempted to obtain visual confirmation of a bird's status once detected (when successful, these were defined as "tracking" observations). We also used handheld telemetry equipment on the western slope to detect emigration from the northern slope, but we were unable to visually confirm most of these detections. During T4, we used a single null-peak telemetry tower on top of Puʽu Mali to determine whether birds were moving (i.e., alive). A bird was considered to be moving when the daily change in its bearing was >5°, but a change of ≤5° for three or more consecutive days triggered a ground search using a hand-held receiver. When no signal was detected from the null-peak tower, we searched for the bird with handheld receivers along the main forest reserve road (R1), along transects established throughout the reintroduction area, and in the vicinity of the bird's capture area on the western slope. Additionally, we searched for the palila without transmitters, and those with expired batteries, in the suitable habitat on the northern slope. Detections without the assistance of telemetry were defined as "re-sight" observations. A variety of behavioral data were recorded when radio-tracking and re-sighting birds.

Survival and persistence in the reintroduction area

Eight weeks after translocation, each bird's fate was categorized as: persisted (bird was still present on the northern slope), emigrated (bird was on the western slope, or detected on the western slope at a later date), dead (bird's remains recovered), or unknown (bird's transmitter was shed or the battery died early). Eight weeks was considered the standard for assessing the persistence of birds on the northern slope because that was the average duration of transmitter batteries. To be classified as persistent for one week, birds had to be present on the northern slope for 7–13 days; to be classified as persistent for eight weeks, birds had to be present for over 56 days. Birds that died before eight weeks or that persisted on the northern slope for longer than eight weeks were excluded from the analysis of mean emigration time. Four birds that were translocated twice, in two different years, were excluded from analysis on their second translocation. T3 was also excluded from statistical comparisons among translocations because of its small sample (n = 4 birds). Thierry Work (DVM, U.S. Geological Survey) necropsied all translocated or control birds that died.

Radio-tracking data were more comparable among translocation trials because our re-sight monitoring effort varied over time. Even so, the re-sight data provided additional important insight into individual persistence and behavior; therefore, bird fates were classified using both types of data. Inference about the long-term (more than eight weeks) persistence of birds was based upon re-sight data because of the difficulty in recapturing birds and replacing their transmitters after their release on the northern slope.

We used ANOVA models to test for differences in mean emigration times among translocations and source populations and t-tests for differences between sexes and among age classes. Significant ANOVA effects were subjected to simulation-based *post hoc* tests (Edwards and Berry 1987). Birds whose age or sex was difficult to determine were not included in analyses of age or sex.

We used logistic regression to examine the effect of age, sex, source area, and northern slope palila abundance on whether a bird persisted for at least eight weeks on the northern slope. Population abundance on a date was defined as the total number of birds detected by tracking or re-sighting in the 32 days prior to that date. Population on the day of translocation and the maximum population in the first week after translocation were both tested as predictors of eight-week persistence.

Home range, habitat utilization, and movement between western and northern slopes
We examined the movement patterns of translocated palila to understand how they responded to their new environment in terms of home range and habitat utilization. During T1–T3, we determined the home range of birds, which we defined as the area used by an individual for foraging, roosting, and socializing during the life of the radio transmitter (nominally eight weeks). Using the Animal Movement Analyst ArcView extension (Hooge and Eichenlaub 1997, ESRI 1999), 95% kernel home ranges (Worton 1989) were calculated from daily point locations for each bird. We estimated home range size by locating birds in random order throughout the day, marking locations, and obtaining GPS coordinates (± 4–10 m). During T2 and T3, we monitored birds more frequently during the first 48 hours after release to increase our ability to detect problems related to transport. We compared the home range size of birds during and after the first 21 days in the reintroduction area using a t-test. During T4–T6, we did not obtain enough precise locations to compare home ranges during and after the first 20 days.

We examined differences in the size of the area used by individual palila of different ages, sexes, translocation trials (T1–T6), and slopes (north vs. west) using both kernel density estimates (KDE; Worton 1989, Seaman and Powell 1996, Seaman *et al.* 1999, Marzluff *et al.* 2004) and local convex hulls (LCH; Getz and Wilmers 2004, Getz *et al.* 2007). Although home range indicates the exterior boundary of movement (Burt 1943), the utilization distribution generates the frequency distribution of locations (Jennrich and Turner 1969, Van Winkle 1975). Palila do not display stereotypical territorial behavior and typically only defend their nest site (van Riper 1980, Fancy *et al.* 1993), so using a utilization distribution framework avoids *a priori* biological judgments about the spatial use of habitat. We did not calculate minimum convex polygons because of their unreliability and unpredictable relationship among sample size, sampling regime, and variance (Börger *et al.* 2006).

Only one tracking observation (chosen at random) was used for each bird per day. This served to standardize our uneven sampling intensity across birds and translocations and provided biological, if not statistical, independence and minimized autocorrelation (De Solla *et al.* 1999, Blundell *et al.* 2001, Barg *et al.* 2005). The bivariate fixed KDE in Hawth's Tools (Beyer 2004) was used to calculate the utilization distribution, then the area of the isopleths in 10% increments was calculated using XTools Pro 5.2.0 in ArcGIS 9.3 (Data East 2008, ESRI 2008).

After examining increasingly large subsamples of palila with 40–69 total locations (*n* = 16 birds), we determined our KDE reached an asymptote at ≥30 observations. Over 30 locations were logged for 20 translocated birds, so we calculated individual KDE and LCH areas for only these birds. Because of the problems in using least squares cross-validation as well as a smoothing parameter to control the width of the kernel function (h_{ref}; Seaman and Powell 1996, De Solla *et al.* 1999, Blundell *et al.* 2001, Hemson *et al.* 2005, Huck *et al.* 2008), we generated isopleths from a wide range of smoothing parameters and selected h = 150 as appropriate to our data, applying it uniformly to all utilization distribution calculations (Silverman 1986, De Solla *et al.* 1999, Pope *et al.* 2004, Huck *et al.* 2008). The outer boundaries of a utilization distribution are difficult to estimate precisely, so for comparisons among groups we used the area of the 50% and 90% isopleths to minimize potential bias (Seaman *et al.* 1999, Börger *et al.* 2006).

Local convex hulls sometimes perform better than KDE in patchy habitat, particularly where there are "holes" in the potential habitat (Getz and Wilmers 2004, Getz *et al.* 2007, Huck *et al.* 2008), such as we found on the northern slope of Mauna Kea. Therefore we compared the results from the KDE techniques with the newer LCH. We calculated LCH areas for the 16 birds with at least 40 observations for a range of nearest neighbors using the method and software described in Getz *et al.* (2007) and Program R (R Development Core Team 2008). We chose k = 20 nearest neighbors as the point where the areas stabilized and used that value for all further LCH calculations.

Although there are weaknesses and limitations in pooling observations across individuals (e.g., Aebischer *et al.* 1993), we combined locations within categories and compared differences in the utilization distributions among the different translocations, sexes, ages, and seasons because there were few birds with sufficient observations. We included the control palila released on the western slope, as well as birds that returned to the western slope after translocation, to examine differences in how translocated birds used the northern versus the western slopes of Mauna Kea. To qualitatively evaluate changes in the utilization distributions of individual palila through time, we examined the KDE results from 16 translocated and 6 captive-reared birds for which there were at least 10 locations both during and after their first 21 days in the reintroduction area. Palila that returned to the western slope were detected there 20 days (median) after they were last detected on the northern slope (mean = 49 days, range = 1–325 days), and 20 days seemed an adequate period for birds to have explored and become familiar with the reintroduction area.

Movement back-and-forth (commuting) between the source and reintroduction areas was documented by multiple telemetry detections of a bird on the western slope with support from either visual confirmation or inference from multiple-month gaps in detecting the bird on the northern slope. Although telemetry detections alone were not considered unquestionably reliable for determining a bird's presence in either location, commuting was the most likely explanation for long gaps between detections because of the strong tendency for birds to occupy only a few habitat patches on the northern slope.

Roosting behavior

Due to the unexpected mortality of some T2 birds, we monitored roosting behavior and assessed the characteristics of roost sites to determine the potential threat of predators to translocated palila in an unfamiliar environment. Night roost usage was examined during October 1997–December 1998 (T2, T3) and November 2006–April 2007 (T4–T6). During T2 and T3, we tracked birds at dusk until they settled in their roost trees. We recorded the tree species, estimated the height of the bird in the tree (when we could see the bird), the bird's distance from the edge of the canopy, number and species of roost mates, and any behavior observed prior to roosting. During 2006–2007, we used radio-telemetry to track birds before dawn to find their roost trees, but we did not characterize the habitat. This effort focused on the locally produced (F1 generation) birds, which we suspected were using communal roost trees. For those birds with reliable utilization distributions (i.e., ≥30 daytime locations), we compared the distribution of their night roosts to their 50% and 90% isopleths (n = 9 northern slope birds, and n = 6 western slope birds). The mean-use centroid was calculated for birds with more than five daily locations using ArcGIS 9.3, then the distances to all night roosts were calculated for each individual (n = 15 northern slope birds, n = 14 western slope birds; Beyer 2004). Roost fidelity of each bird was measured by dividing its total number of roost locations by the number of different sites it used; a value of 1.0 indicated that the bird was detected at a different roost site on each occasion, whereas higher values indicated some frequency of repeated use of the same roost site.

We assessed roost tree characteristics in April 1999 using data from the māmane-dominated forest on the northern slope and two western slope study areas: the māmane-dominated Mauka grid and naio-dominated Ahumoa grid (see Figure I.2). We chose 10 trees from these three regions (30 trees) known to have been used for roosting by palila within the last year, hereafter termed focal roost trees, and examined the tree and the surrounding area (within 11.3 m). A second, paired tree was selected for comparison (another 30 trees, 60 total) that was within 10% of the height, and similar in structure, foliage density, and vigor to the focal roost tree. The paired tree was located at the same elevation (±15 m) between 22.6–100 m away. This represented an area that was close enough to the focal roost tree to be considered similar, yet far enough away to avoid encountering the same microhabitat characterized around the focal roost tree. For each focal roost and paired tree the following variables were recorded: structure and branching class, diameter of all stems (≥5 cm), number of minor stems (<5 cm), canopy dimensions, canopy overlap, tree vigor, and presence of vines (*Stenogyne microphylla*).

We also sampled the structure and composition of the vegetation within a 0.04 ha circular plot centered on both the focal roost and paired trees (James and Shugart 1970), the 'roost tree patch.' We divided each plot into quarters with tape-measures radiating from the center along the cardinal axes. Point-intercept measurements were taken at 1-m intervals along each transect (n = 44 points per plot), and all vegetation touching the pole in five height categories (0, 0–0.5, 0.5–1, 1–2, and >2 m) was identified to species. We measured canopy cover with a densiometer at 3, 6, and 9 m along the four tapes (Lemmon 1956). The distance to the nearest tree in each of the plot's quarters was determined in two ways: base of the focal roost tree to the base of the nearest tree, and outermost edge of the canopy of the focal roost tree to the outermost edge of the canopy of the nearest tree. Shrubs (woody species <2 m tall) were identified to species in each of the plot quarters and classified according to size. We characterized all trees with ≥50% of their base inside the study plot. We also recorded a short description of the plot, including a complete species list, and noted the presence of ungulate sign. Discriminant function analysis and factor analysis (Dray and Dufour 2007) were used to identify which vegetation parameters differed most between focal roost and paired trees, as well as to attempt to correctly classify the plots at each tree type from the three sample areas.

Because the paired trees were selected to be closely similar in structure to the focal roost trees, we also compared focal roost tree characteristics to the forest on the western slope of Mauna

Kea at the landscape scale. A series of 40 x 40 m plots (0.16 ha) were surveyed around Mauna Kea in 1999–2001 (see Chapter 25: Vegetation Survey in Palila Critical Habitat). We compared the mean of the focal roost tree patch to that of the forest at the landscape scale using all plots that were within 750 m of any focal roost tree (61 plots in the western māmane forest, 46 in the western mixed forest, and 21 in the northern māmane forest). We examined the differences in: 1) the maximum canopy height, 2) mean canopy area per tree, 3) the forest density, calculated as the number of stems per hectare, and 4) the percent cover based upon the point-intercept measurements.

Reproduction

We recorded any behavior indicating that translocated birds were mating and nesting, although we seldom conducted systematic searches for nests, even prior to 2007, when there was relatively high capacity for monitoring. When nests were found, we observed the nest contents with pole-mounted mirrors during breaks in parental nest attendance, and we observed behavior at the nest from blinds set up ≥20 m away. Estimates of reproductive productivity were upper limits because we did not detect all breeding failures at the nest, egg, or nestling stages and we assumed that pairs accompanied by fledglings had suffered no earlier losses of eggs or nestlings. We assumed that fledglings that were fed by an accompanying adult were the offspring of that adult, although in one instance, we suspected that a fledgling was fed by a male nest helper. Additionally, after 2007, when we were unable to monitor the colony closely, we assumed that fledglings were the offspring of accompanying adults, even if we did not observe the fledgling being fed or begging from the adult. Fledglings are present in the same tree with adults or other juveniles only 36% of the time (Miller 1998), so observations of fledglings and adults together more likely signified a familial connection rather than some other form of social attraction or fortuitous association around clustered resources.

Release of captive-reared palila

In a separately funded but cooperative program at the Keauhou Bird Conservation Center (KBCC), the San Diego Zoo Institute for Conservation Research (SDZICR) raised palila in captivity and then conducted soft releases (e.g., using on-site hack towers and supplemental feedings) near the location where translocated palila were released. This program released a total of 28 palila: 10 in December 2003, 5 in December 2004, 6 in December 2005, and 7 in March 2009 (Lieberman 2005, Lieberman and Kuehler 2009, Keauhou Bird Conservation Center unpublished data). These birds had no experience living in wild habitats on Mauna Kea; therefore, they were treated as a separate category ("captive-reared") and were not included with translocated palila in analyses of survival, reproduction, or persistence in the reintroduction area. After eight weeks of monitoring by SDZICR, we attached new transmitters whenever possible, and continued monitoring the survival, reproduction, and behavior of these individuals.

Results

Demographics of Translocated and Control Birds

We captured 447 palila on the western slope of Mauna Kea in six episodes during 1997−2006 (Table 2.1). Based on plumage characteristics (Jeffrey *et al.* 1993), the age composition of these birds was dominated by older birds: 26 (6%) HY, 130 (29%) SY, 46 (10%) AHY, 242 (54%) ASY, and 3 (1%) unknown (Table 2.2). The sex ratio was male-biased: 174 (39%) females, 215 (48%) males, and 58 (13%) unknown.

Of the 447 palila caught, we translocated 188 (173 with transmitters) to the northern slope during six trials between February 1997 and April 2006 (Table 2.1). We translocated birds

Table 2.1. Capture effort and yield and translocation rates during translocations 1–6.

	T1	T2	T3	T4	T5	T6
Capture period	Feb–Mar 1997	Oct 1997–Mar 1998	Nov–Dec 1998	Apr 2004	Mar–Apr 2005	Mar–Apr 2006
Number of nets	34	30	13	15–35	30–56	30–56
Total net-m-hours[1]	27,948	33,540	12,000	23,898	36,328	24,868
Total palila captured	91	110	52	48	103	43
Total palila translocated[2]	25	24	4	32 (13)	75 (2)	28
Total palila controls	12	12	2	4	0	0
Palila captured per 1,000 net-m-hours	3.26	3.28	4.33	2.01	2.83	1.73
Net-m-hours per translocated bird	1,118	1,398	3,000	747	484	888
Total palila captured per palila translocated	3.6	4.6	13.0	1.5	1.4	1.5

[1] Total net-m-hours = the total length (m) of mist-nets open multiplied by the time (hours) in operation

[2] Numbers in parentheses indicate how many palila did not have radio-transmitters; if no second number is shown then all birds had transmitters.

before the period of peak breeding (Banko *et al.* 2002b) and generally when māmane pods were most abundant (Banko *et al.* 2002a; Figure 2.1).

Of the 188 translocated birds, 81 were female (F), 92 were male (M), and 15 were unclassified (U; Tables 2.2 and 2.3). The proportion of males to females varied considerably among trials but was relatively even during T1–T3. The age distribution of the translocated palila was: 13 HY (3 F), 80 SY (56 F), 1 AHY (1 M), 92 ASY (21 F), and 2 undetermined age (1 F). Mostly young birds (88% HY and SY: 12% ASY) were translocated during T1–T3, but older birds (35% HY and SY: 65% ASY) were moved more frequently during T4–T6 (Tables 2.2 and 2.3, Figure 2.2).

Only SY palila were translocated in T1, therefore no males were of breeding age (Pratt *et al.* 1997). The sex distribution of breeding-aged palila was nearly even in T2, but males greatly outnumbered females in T4 and T6, and females greatly outnumbered males in T5 (Figure 2.3). Nevertheless, the ratio of mature females to males was nearly even (59F:62M) over the course of T4–T6, when many palila of breeding age were translocated in the hope of stimulating breeding in the reintroduction area.

There was a threefold difference between our lowest (T3) and our highest (T5) rates of capture effort (net-m-hours) among translocation trials (Table 2.1), which led to a difference in the daily rate of translocating birds. As a result, the number of translocated birds present in the release area at any given time varied, but the most was 86 during T5.

Of the 259 palila that were captured on the western slope but not translocated, we released 30 as controls during T1–T4 (Table 2.1). We released an additional 153 that were not the desired age or sex, 31 that exhibited signs of breeding, and 10 that seemed stressed or behaviorally unsuitable for transport. We disqualified 35 others for translocation for various other reasons,

Table 2.2. Distribution of sex and age of all 447 palila captured, translocated, and released as controls or unmonitored birds during six translocations (T1–T6) on Mauna Kea.

	T1	T2	T3	T4	T5	T6
[1]Palila captured—F:M:U						
HY	0	0:1:16	0:0:7	0	0	0:0:2
SY	20:10:14	10:3:6	1:2:1	3:0:0	44:3:5	7:1:0
AHY	0	10:16:0	5:14:0	0	0	0:1:0
ASY	17:28:1	13:32:2	9:13:0	8:35:2	19:31	7:25:0
U	0:0:1	0:0:1	0	0	1:0:0	0
Total	37:38:16	33:52:25	15:29:8	11:35:2	64:34:5	14:27:2
Palila translocated—F:M:U						
HY	0	2:6:0	1:2:1	0	0	0:1:0
SY	10:9:6	7:2:0	0	3:0:0	31:3:4	5:0:0
AHY	0	0:1:0	0	0	0	0
ASY	0	1:5:0	0	4:23:2	13:22:1	3:17:1
U	0	0	0	0	1:0:0	0:1:0
Total	10:9:6	10:14:0	1:2:1	7:23:2	45:25:5	8:19:1
Palila controls—F:M:U						
HY	0	0:0:6	0:0:2	0	0	0
SY	6:1:5	2:1:0	0	0	0	0
AHY	0	0	0	0	0	0
ASY	0	0:3:0	0	0:4:0	0	0
U	0	0	0	0	0	0
Total	6:1:5	2:4:6	0:0:2	0:4:0	0	0

[1] F = female, M = male, U = unclassified sex; HY = hatch year, SY = second year, AHY = after hatch year, ASY = after second year, U = unclassified age (see Jeffrey *et al.* 1993 for details on how age and sex were determined in the field; sex of most translocated palila was verified by DNA analysis of feather pulp [Patch-Highfill 2008]).

including poor weather at the reintroduction area or logistical problems. The sex and age distribution of control birds was 8 F, 9 M, and 13 U; 8 HY, 15 SY, and 7 ASY (Table 2.2). The control birds were younger overall compared with the translocated birds: HY birds composed 27% of the control group and only 1% of the translocated group, whereas ASY birds composed 23% of the control group and 49% of the translocated group (Table 2.4). Because the sex of young palila is difficult to determine (Jeffrey *et al.* 1993), the gender of 43% of the control birds was unknown, whereas we could not determine the gender of only 8% of the translocated birds.

Response to Holding and Transport

Translocated palila were released at the reintroduction site within nine hours of capture. Many birds ate māmane flowers and pods that we provided during transport, and though some birds moved about briefly inside their cages, most perched quietly during transport. The mean time between capture and release at the reintroduction site was similar for T1 and T2. Holding time was slightly longer in T3 because we allowed the birds to acclimatize to their carriers for 15 minutes prior to transport and stopped to check birds three times along the way before the final

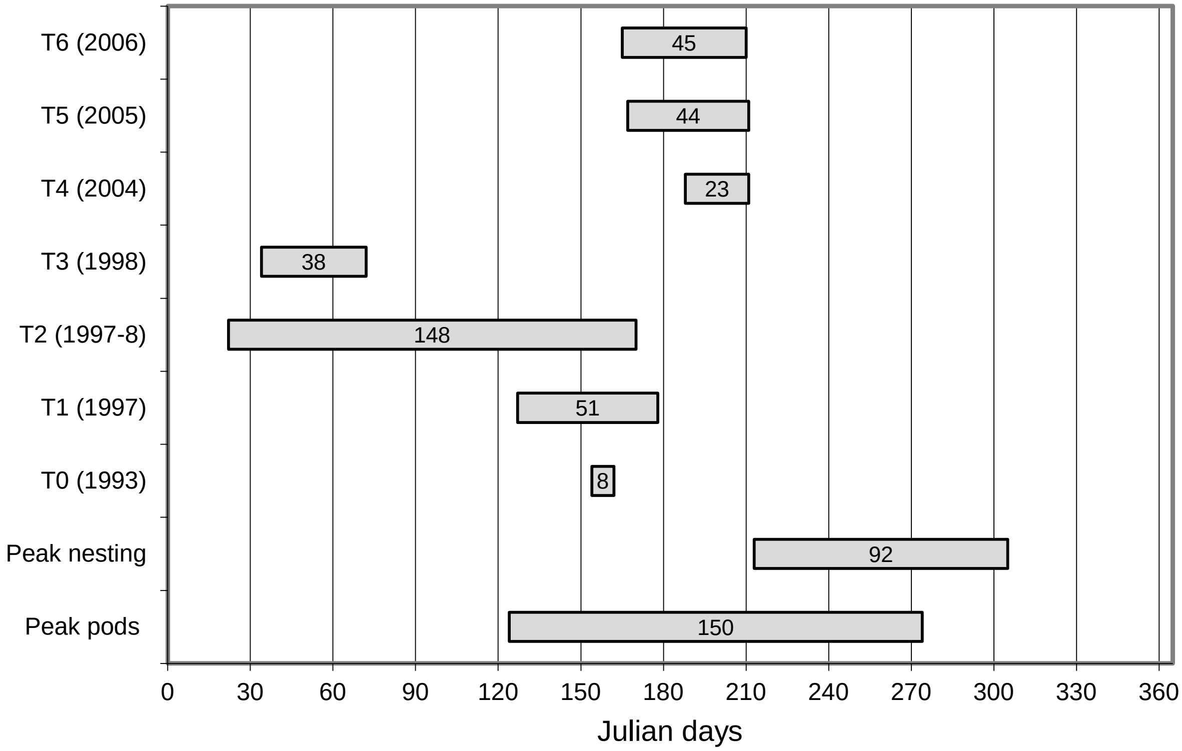


Figure 2.1. Timing of translocation trials (T1–T6) to the northern slope of Mauna Kea and the 1993 translocation (T0) to the eastern slope of Mauna Kea (Fancy *et al.* 1997). Palila were translocated before the time of peak breeding and generally when māmane pods were abundant. Numbers in the boxes are the total number of days represented.

inspection prior to release (Table 2.5). The mean holding time was substantially longer during T4−T6 because we postponed transport until 1200 hours, or in some cases 1300 hours.

All birds responded well to transport during T1−T3, but 4% (2/53) of translocated birds died within 24 hours of release at the reintroduction site. Two palila from T2 died soon after translocation. One palila (T2-07) died of trauma caused by a broken sternum that lacerated the heart. This injury may have been inflicted during netting or transportation. Despite attempts to save the bird, it died shortly after release. Palila T2-08 was found dead on the morning after its release within 40 m of the release site. A necropsy performed by Dr. Work (DVM) revealed a perforated gut. It was not determined whether this was caused by trauma during translocation or was a pre-existing condition. No birds in T3−T6 died within the first 24 hours after translocation, and only one individual exhibited stress at the release site. Intensive avian first aid throughout the night revived this individual, and in the morning she was released in the reintroduction area, where she was regularly seen for the next three months. We administered lactated Ringer's fluid to 31% (10/32) of the birds released in T4, 12% (9/75) in T5, and 25% (7/28) in T6, and none seemed to suffer any ill effects from the treatment.

Birds usually, but not always, lost weight from the time of capture to the time of release (Table 2.5). Differences in weight change were significant among the translocations (ANOVA, $F_{4,178}$ = 4.58, P = 0.001), but the early translocations (T1–T3) involved mostly HY and SY birds that

Table 2.3. Age and sex distribution of palila translocated to the northern slope of Mauna Kea during trials T1–T6. Age and sex determinations were based on Jeffrey *et al.* (1993), and sex was verified for most birds using DNA from feather pulp (Patch-Highfill 2008). HY = hatch year, SY = second year, AHY = after hatch year, ASY = after second year, U = unclassified.

	Female					Male						Unclassified sex				
	HY	SY	ASY	U	Subtotal	HY	SY	AHY	ASY	U	Subtotal	HY	SY	ASY	Subtotal	TOTAL
T1		10			10		9				9		6		6	25
T2	2	7	1		10	6	2	1	5		14					24
T3	1				1	2					2	1			1	4
T4		3	4		7				23		23			2	2	32
T5		31	13	1	45		3		22		25		4	1	5	75
T6		5	3		8	1			17	1	19			1	1	28
TOTAL	3	56	21	1	81	9	14	1	67	1	92	1	10	4	15	188

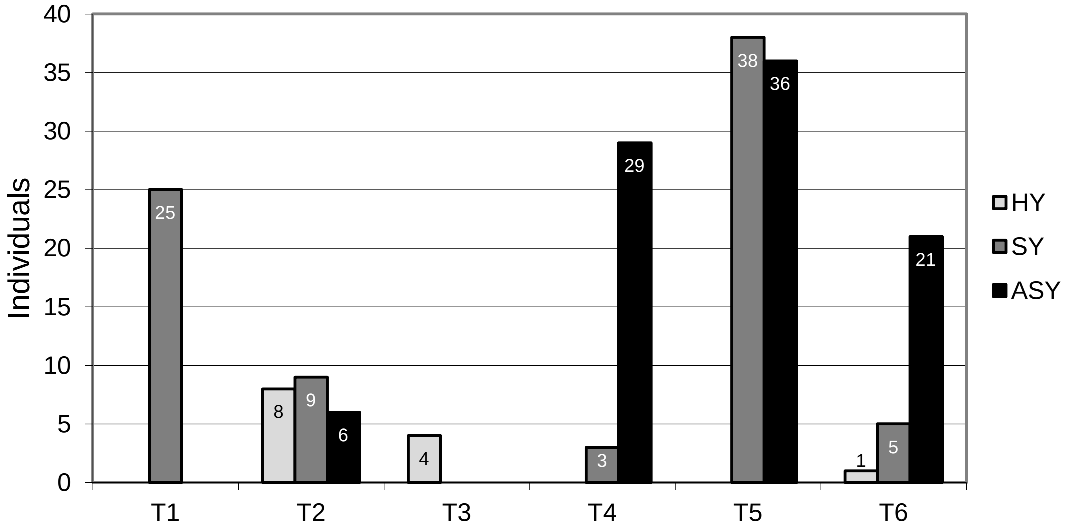


Figure 2.2. Age distribution of 185 palila translocated during T1–T6. Shown are hatch-year (HY, *n* = 13), second-year (SY, *n* = 80), and after-second-year (ASY, *n* = 92) age classes (Jeffrey *et al.* 1993). Not shown are after-hatch-year (*n* = 1) and unclassified (*n* = 2) age classes.

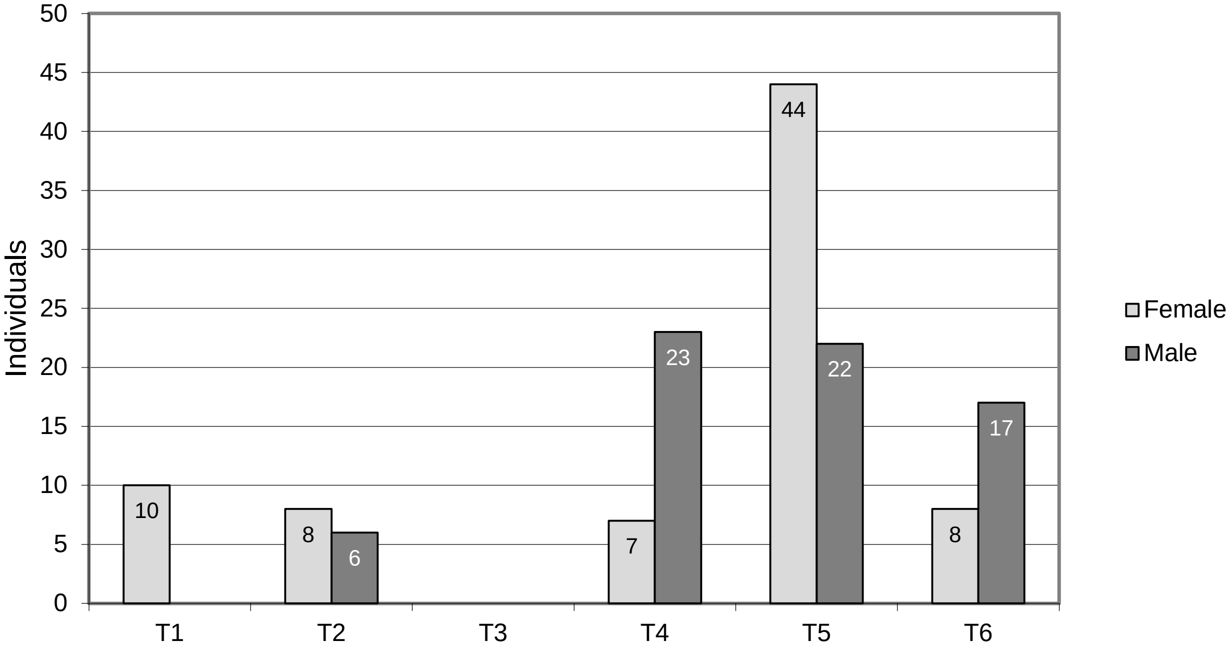


Figure 2.3. Distribution of breeding-aged palila translocated during six translocations (T1–T6) to the northern slope of Mauna Kea. Only second-year palila were translocated in T1, therefore no males were of breeding age. Only in T2 and T5 were there more females than males.

Table 2.4. Proportionate age and sex distribution of palila monitored as controls (*n* = 30) or translocated (*n* = 188). Values are percentages.

Age class	Control	Translocated
HY	26.7	6.9
AHY	0.0	0.5
SY	50.0	42.6
ASY	23.3	48.9
U	0.0	1.1
Sex		
F	26.7	43.1
M	30.0	48.9
U	43.3	8.0

were transported soon after capture, whereas the later translocations (T4–T6) involved mostly ASY birds that were moved as a group in the late morning or early afternoon. Changes in weight were significantly less during T4–T6 than during T1–T2 (ANOVA, $F_{1,181}$ = 11.42, *P* = 0.009). Over the six translocation trials, weight change was inversely related to holding time (linear regression, r^2 = 0.02, *P* = 0.04; Figure 2.4). Although this relationship explained a

Table 2.5. Holding time and relative weight change for translocated palila. Negative values for range of weight change are shown in parentheses. Values for Fancy *et al.* (1997) mean and range of holding time were calculated from raw data (U.S. Geological Survey unpublished data); mean and range of weight change calculated from Table 1 in Fancy *et al.* (1997).

	Mean holding time ± SE (hour)	Range of holding times (hour)	Mean weight change ± SE (%)	Range of weight change (%)
T1	3.3 ± 0.07	2.7–4.2	-6.4 ± 0.7	(13.7)−3.0
T2	3.4 ± 0.06	2.9–3.9	-6.8 ± 0.4	(3.5)–(10.5)
T3	3.6 ± 0.08	3.4–3.8	-6.2 ± 2.4	(2.1)–(11.6)
T1–T3	3.4 ± 0.05	2.7-4.2	-6.6 ± 0.4	(13.7)−3.0
T4	6.5 ± 0.26	3.7–8.6	-3.3 ± 0.6	(10.2)−3.5
T5	6.0 ± 0.12	3.8–8.2	-4.5 ± 0.8	(17.9)−24.9
T6	5.7 ± 0.21	3.7–7.4	-1.6 ± 1.1	(9.6)−16.6
T4–T6	6.0 ± 0.10	3.7–8.6	-3.6 ± 0.5	(17.9)−24.9
Fancy *et al.* (1997)	36.0 ± 3.95	1.3–91.1	10.2 ± 1.1	(22.6)−11.1

negligible amount of the biological variation, it indicated that holding and transporting palila for over eight hours resulted in minimal impacts to their health.

Relative weight change during translocation was significantly affected by age (ANOVA, $F_{2,181}$ = 8.06, $P < 0.004$) and sex (t-test, t = -2.44, $P = 0.016$). Hatch-year birds lost 6.1% of their capture weight (n = 13 birds), second-years lost 5.9% (n = 80), and after-second-years lost 2.9% (n = 91). When the effects of age across all translocations were compared with pair-wise post-hoc tests, significant differences were evident only between ASY and SY birds. Males (n = 95) lost 3.5% of their capture weight during translocation, which was significantly less than the 5.4% lost by females (n = 82). However, the age and sex of translocated palila were highly skewed over all translocations as well as the early and late trials (e.g., ASY males were over three times more abundant than ASY females, and SY females were over three times more abundant than SY males; Table 2.3). An ANOVA model with age, sex, and translocation class (early vs. late), all two- and three-way interaction terms, and holding time as a covariate revealed that the only significant factor associated with weight loss was early (T1–T3) versus late (T4–T6) translocations (ANOVA, $F_{10,163}$ = 2.08, $P = 0.029$), which was likely due to different transport protocols.

Palila that were held longer tended to eat more of the māmane pods and flowers provided during T1 and T2 (n = 32 birds; $r^2 = 0.22$, $P = 0.007$), and birds were more likely to eat the longer they were held. Nevertheless, weight change was not related to the amount of food eaten ($r^2 = -0.10$, $P > 0.5$), suggesting that weight loss was due to stress or other factors rather than food consumption. Feces from palila held for an intermediate amount of time (180–240 minutes) were more likely to contain <25% or >75% urates, indicating that these birds were calorie deficient (Figure 2.5). The mean proportion of feces consisting of 50% urates was highest in those birds held for the shortest and longest periods, and the number of feces produced was relatively stable regardless of holding time ($r^2 = 0.04$, $P = 0.21$).

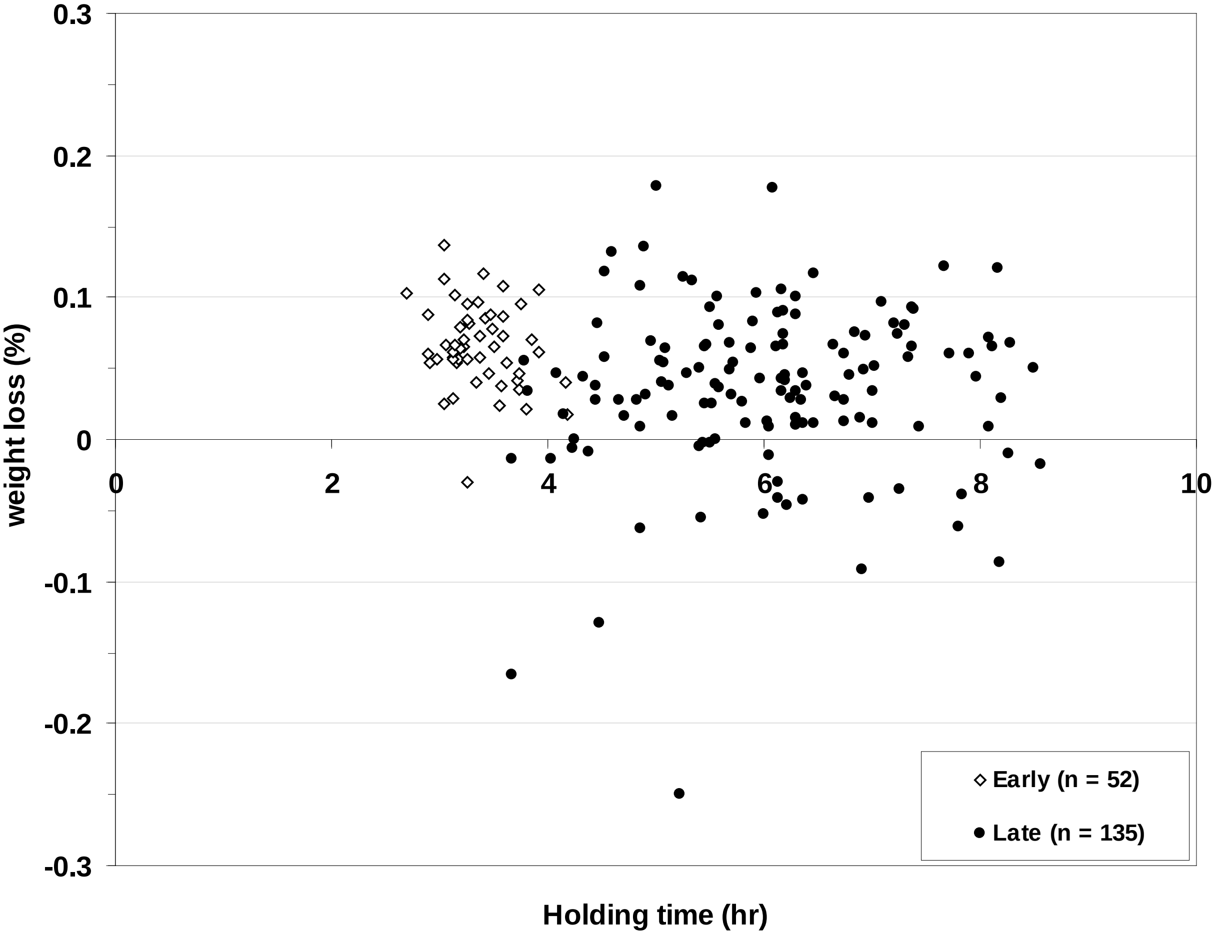


Figure 2.4. The relationship between holding time and relative weight loss for translocated palila. We conducted the early translocations (T1–T3) in 1997–1998 and the late ones (T4–T6) in 2004–2006. Only birds that had holding times and weight change data collected were included, so the sample sizes are less than the total translocated in each class. A negative relative weight loss indicates that the bird gained weight during the holding period.

Short-term (Eight-week) Fate of Translocated Birds and Controls

Our ability to accurately determine rates of survival and emigration was sensitive to the availability of staff, especially during T1−T4 and T6, when we did not use telemetry towers. Having more staff during T2−T3 allowed us to spend over twice as much time tracking birds than during T1. Using radio telemetry towers during T4 and T5 allowed us to obtain more locations per bird. During T4 (7 April−18 June 2004), we recorded 533 locations for 32 birds (mean = 16.6 locations per bird, range = 1–46 locations) using the null-peak telemetry tower on Pu'u Mali, and 86 additional locations were obtained for 25 birds with hand-held telemetry. During T5 (24 March–23 June 2005), we recorded 809 locations for 58 birds (mean = 13.9 locations per bird, range = 1–34 locations) using the null-peak telemetry tower, and 221 additional locations of 55 birds were obtained using hand-held telemetry. During T6 (15 March–22 June 2006), we recorded 173 locations for 28 birds (mean = 6.6 locations per bird, range = 1–13 locations) by hand-held telemetry only.

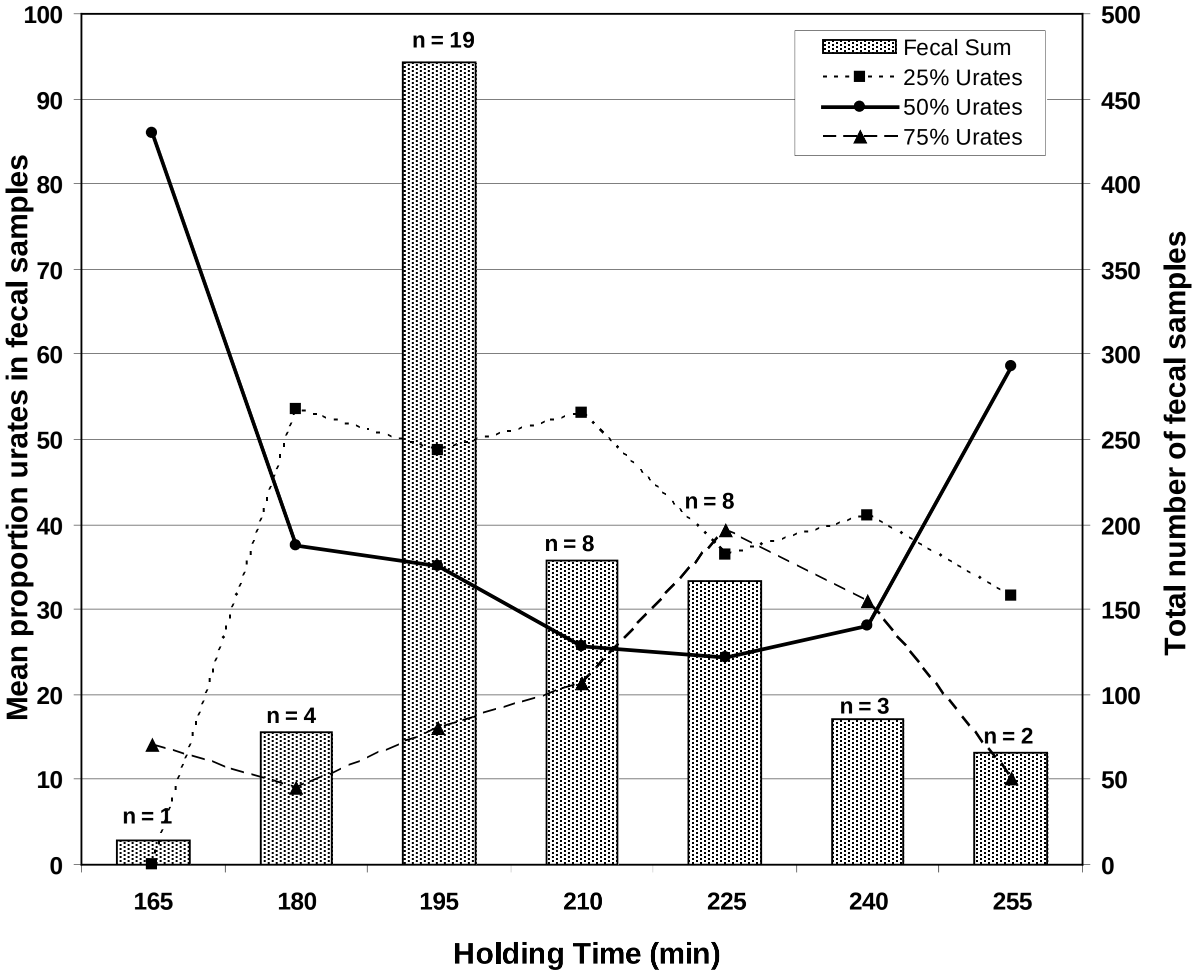


Figure 2.5. Proportion of urates in fecal samples of translocated palila collected shortly after capture until release, 1997–1998. The mean proportion of <25%, 50% (all samples ≥25% and ≤75%), and >75% is given on the left y-axis for the 45 birds with fecal data. Bars (scale on right y-axis) indicate the total number of fecal samples collected for each time category with the number of palila translocated at the top of each bar.

The survival and behavior of palila were monitored in the reintroduction area for eight weeks by radio-tracking and by a combination of radio-tracking and re-sighting. Based on the more conservative method (radio-tracking only), 25% (*n* = 44) of birds persisted on the northern slope for at least eight weeks, but when re-sighting data were also considered, we determined that 34% (*n* = 59) remained in the release area for eight weeks (Table 2.6, Figure 2.6). Based on telemetry and re-sighting, eight-week persistence ranged from 21% (T2) to 50% (T3), but rates of emigration and mortality were more variable between trials (Table 2.6, Figure 2.7). Rates at which translocated birds returned to the western slope were similar irrespective of monitoring method: 20% (*n* = 35) by radio-tracking only and 21% (*n* = 36) by radio-tracking and re-sighting (Table 2.6).

Table 2.6. Individual fates eight weeks after translocation. Birds with radio transmitters were tracked regularly to provide a standardized effort to determine their status. Opportunistic re-sights provided additional information but may be biased by individual bird behavior.

	Radio-tracked observations only				Including re-sight observations			
	Persist	Return	Dead	Unknown	Persist	Return	Dead	Unknown
T1	10	13	0	2	10	13	0	2
T2	5	3	14	2	5	3	14	2
T3	2	2	0	0	2	2	0	0
T4	6	7	2	17	8	7	2	15
T5	16	8	6	32	27	8	6	21
T6	5	2	4	15	7	3	4	12
Total	44	35	26	68	59	36	26	52

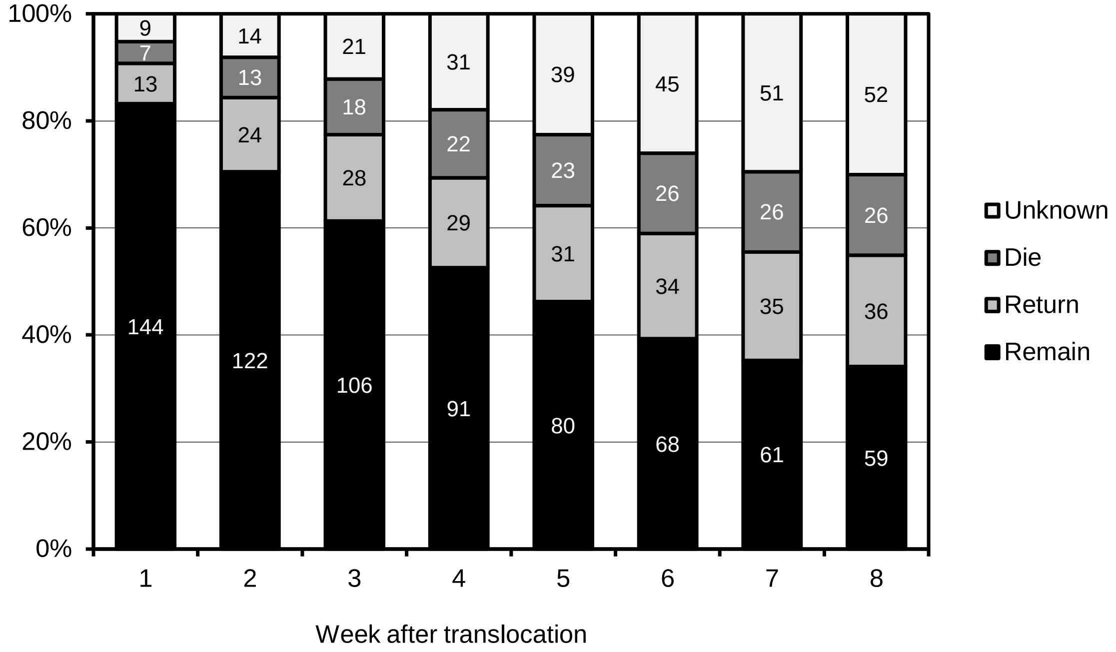


Figure 2.6. Results of all translocation trials (T1–T6) after eight weeks for 173 radio-tagged palila captured on the western slope and translocated to the northern slope of Mauna Kea. Numbers of palila are shown within each bar segment.

The highest mortality occurred during T2 when 14 (58%) of the 24 translocated birds died, but 0–15% of birds died during other trials and the overall mortality rate was 15% (n = 26). An additional bird died at least nine days after returning to the western slope, but we classified it as an emigrant. Predation by raptors and introduced small mammals was the primary cause of mortality ($n \geq 9$), but radio antenna entanglement likely contributed to mortality during T2 and T6 (Dougill *et al.* 2000), and at least two birds died of trauma or undetermined causes associated with translocation.

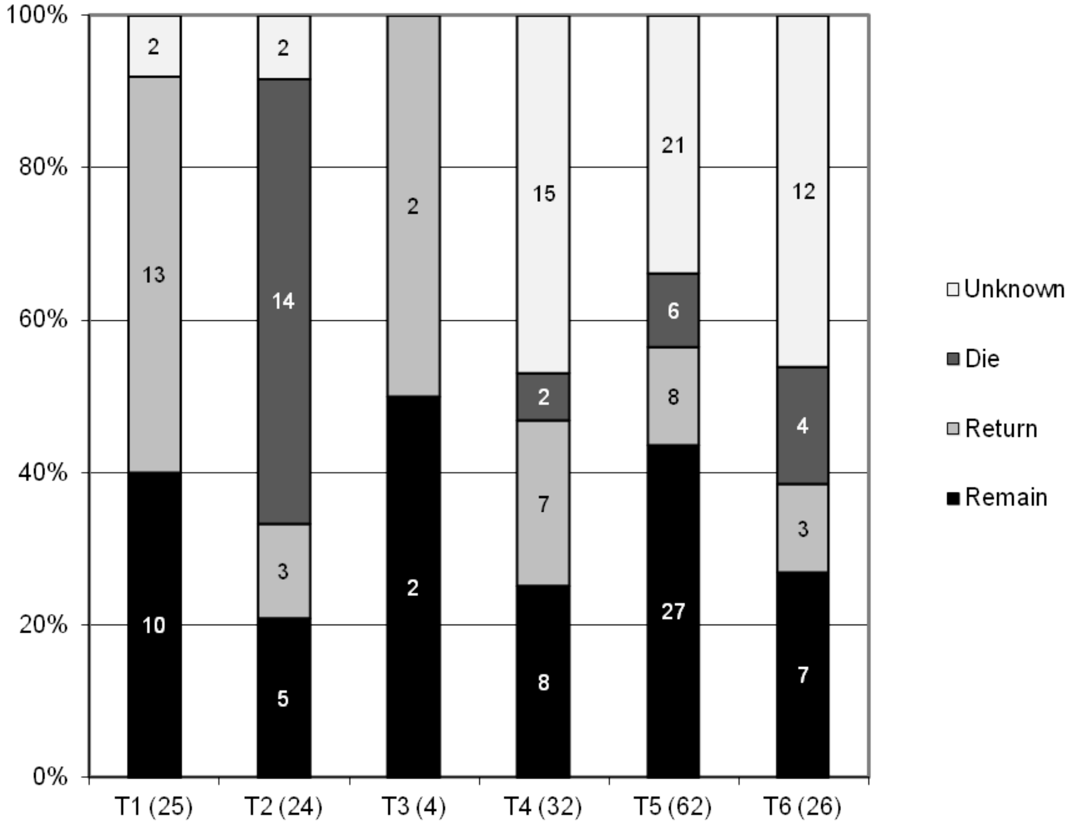


Figure 2.7. Results of individual translocation trials (T1–T6) after eight weeks for 173 radio-tagged palila captured on the western slope and translocated to the northern slope of Mauna Kea. Numbers of palila are shown within each bar segment.

The behavior of control birds was monitored to provide a comparison with the behavior of the translocated birds (Table 2.7). The monitoring intensity was lower on the western slope than it was on the northern slope, but there was no significant difference between the eight-week survival rate for known-fate control birds (8/9 survived) and translocated ones (95/121 survived; Fisher's exact test, *P* = 0.68).

Across all translocations, birds that returned to the western slope within eight weeks remained on the northern slope for an average of 11 days (SE 2.3, range = 0−55) before emigrating. An ANOVA testing for differences between mean emigration times among translocations (T1, T2, T4, T5, and T6) detected a significant effect of trial ($F_{4,93}$ = 3.08, *P* = 0.02), but post-hoc testing failed to detect a significant difference between any two trials. We excluded T3 from all statistical analyses because of its small size; however, three birds remained at least 40, 69, and 73 days on the northern slope while the fourth T3 bird was detected on the western slope six days post-release). Using all the data and extending beyond the eight-week telemetry window, the mean emigration time among the five major trials ranged between 11.0 days (T1, *n* = 15 birds) and 28.4 days (T2, *n* = 5). An ANOVA comparing residency times for only T4−T6, the three most comparable translocations in terms of methods, was significant ($F_{2,75}$ = 3.60,

Table 2.7. Fates of control palila eight weeks after capture and release (% in parenthesis). Controls were tracked opportunistically during breaks in translocation activities. The eight-week fates are provided for comparisons with the translocated birds. The long-term results include additional re-sights and banding data after the eight-week period. Some controls from earlier trials were detected during banding or monitoring efforts in later trials on the western slope.

	Fate ≤8 weeks			Fate >8 weeks		
	Persist	Dead	Unknown	Persist	Dead	Unknown
T1	3 (25)	0	9 (75)	8 (67)	0	4 (33)
T2	4 (33)	1 (8)	7 (58)	8 (67)	1 (8)	3 (25)
T3	1 (50)	0	1 (50)	2 (100)	0	0
T4	0	0	4 (100)	1 (25)	0	3 (75)
Total	8 (27)	1 (3)	21 (70)	19 (63)	1 (3)	10 (33)

$P = 0.03$), and post-hoc testing revealed a significant difference between T4 (mean = 11.1 days, $n = 24$) and T6 (mean = 25.1 days, $n = 15$); T5 residency duration was intermediate (mean = 18.4 days, $n = 39$). There was no trend within trials toward delayed emigration of birds that were moved later and that would presumably have had more opportunities to interact with other palila in the reintroduction area.

Effects of other potential predictors (age, sex, source area, or northern slope palila abundance) on the emigration time of translocated birds during the initial eight-week monitoring period were not significant (all $P > 0.10$), either when analyzed individually or in multivariate models. A t-test comparing emigration time of SY versus ASY birds was not significant ($t_{93} = 0.48$, $P = 0.63$), neither was a test comparing male and female time until emigration ($t_{90} = 1.01$, $P = 0.31$). An ANOVA comparing the three major western slope areas where birds were captured did not indicate a significant effect on time until emigration ($F_{2,91} = 2.04$, $P = 0.14$).

Habitat Utilization, Home Range, and Movement between Slopes

Translocated palila traveled extensively across the reintroduction area soon after their release. Nearly all (>98%) tracking points were located in māmane stands within the forest reserve, whereas 45 points were located in wooded pasturelands up to 3.8 km from the release site. Fifteen birds (five from T1, eight from T2, one from T4, and one captive-reared bird) were detected in the pasturelands: eight SY, four HY, and three ASY. All translocated and captive-reared birds were found within at least one of three relatively distinct habitat patches containing abundant, large māmane trees (Figure 2.8). At least 53 palila of all ages and sexes and representing birds from every translocation except T4 moved between the large eastern habitat patch and the smaller patches that were located to the west. The smaller patches were separated from the large patch by 2.5 km of pūkiawe (*Leptecophylla tameiameiae*) shrubland and sparsely vegetated black ash and ʽaʽā lava. Birds sometimes made daily trips between the large and smaller patches, but they also occupied the smaller patches for foraging, roosting, and nesting (on at least one occasion).

Individual KDE utilization distributions of 20 individual palila (≥30 locations each) overlapped extensively and all individuals included the area surrounding the release site in their core use area (50% isopleths), but use of the smaller habitat patches to the west of the main patch varied among birds. The 90% distributions of T1 and T2 bird locations were more fragmented compared to birds in T3–T6, but 50% isopleths from all trials were similar. Although there was

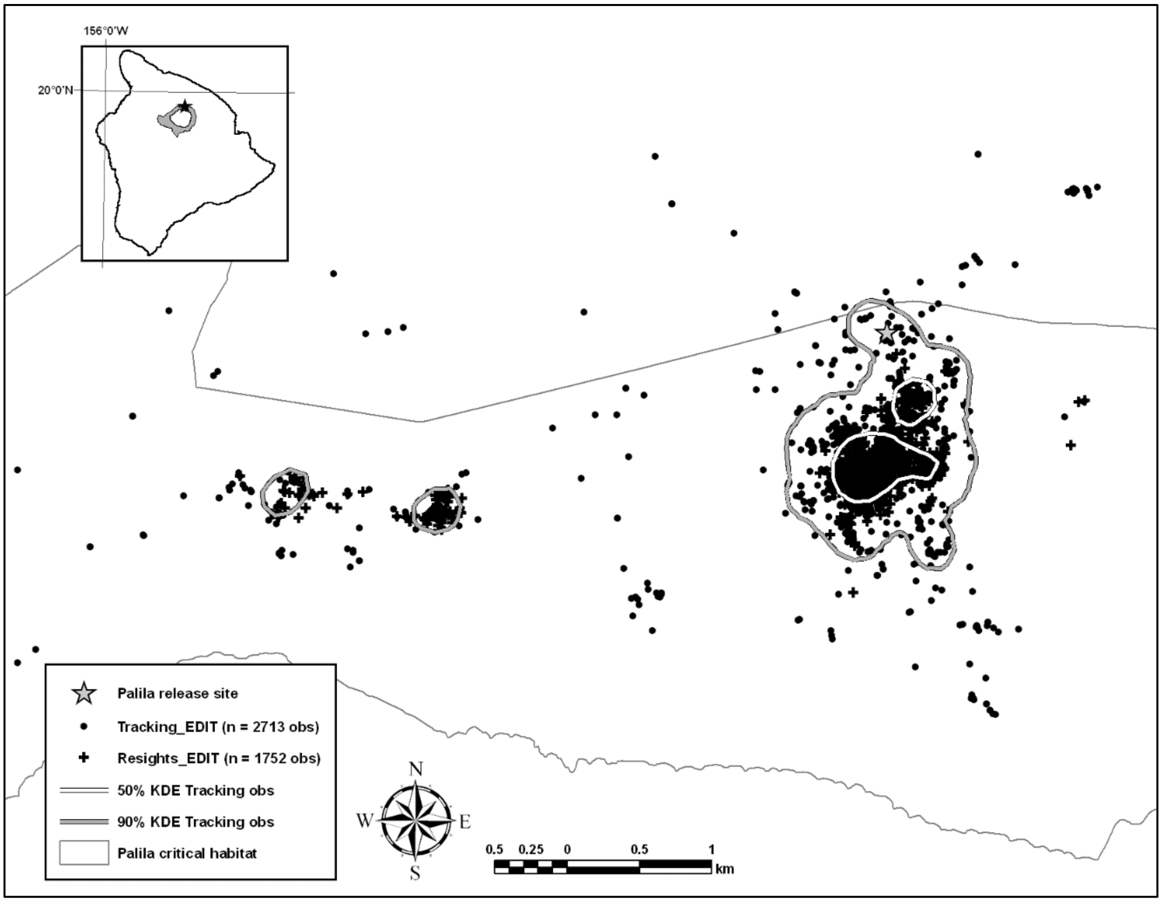


Figure 2.8. Locations of translocated palila detected on the northern slope of Mauna Kea, 1997–2007. Inset shows the island of Hawai'i, Palila Critical Habitat (grey), and the release site (star). The bivariate fixed kernel density estimator in Hawth's Tools (Beyer 2004) was used to calculate the distribution of locations; 50% and 90% isopleths were calculated using XTools Pro 5.2.0 in ArcGIS 9.3 (Data East 2008, ESRI 2008).

more variation in the 90% isopleths, the locations of the 50% isopleths were congruous and centered on the primary habitat patch regardless of the bird's sex, age, or translocation trial. The lack of locations in the smaller habitat patches during summer was distinctive.

The relative size and variation in utilization distributions of 20 individual palila was influenced by their sex, age, and translocation trial, but results were frequently inconsistent (Table 2.8). The rank order of habitat utilization areas estimated by KDE for 90% isopleths agreed with the rank order of 50% isopleth values 65% of the time, but there was lower (50%) correspondence in the rank orders of LCH 90% and 50% isopleth values; also, some LCH 50% isopleth values could not be calculated even with 30 observations. The KDE and LCH estimators generated different values for utilization distribution areas, and while their rank orders were the same for sex and slope, they differed somewhat for age and translocation trial. Females used a larger amount of the habitat than males, and both sexes used larger areas on the western slope (control birds) than they did on the northern slope (translocated birds). Similarly, translocated birds from T2 and T3 used smaller areas on the northern slope than did control birds on the

Table 2.8. The kernel density estimate (h = 150) and local convex hulls (k = 20 nearest neighbors) for 90% and 50% utilization distributions (hectares) of palila. Rank order of kernel and hull estimates is shown in square brackets. More than 30 observations were acquired for each individual, and each observation was separated by at least one day to minimize spatial and temporal autocorrelation. The local convex hull technique cannot calculate small isopleths (i.e., 50%) with low sample sizes, so smaller numbers of individual birds were used in the calculations of some classes. The captive-reared birds were only used within that category; these individuals were not included in the sex or age categories.

				Kernel density estimates (ha)		Local convex hulls (ha)	
Category (slope)	Palila	No. obs.	Period	Mean 90%	Mean 50%	Mean 90%	Mean 50%
T2 (north)	7	300	Oct 97–May 98	27.5 [n-3]	5.4 [n-3]	37.0 [n-1]	4.4 (*n*=5) [n-1]
T2 (west)	7	284	Nov 97–Aug 99	35.5 [w-2]	8.9 [w-2]	52.8 [w-2]	6.3 (*n*=3)
T3 (north)	2	85	Nov 98–Feb 99	29.6 [n-2]	7.5 [n-2]	12.4 [n-3]	1.0 [n-3]
T3 (west)	1	36	Dec 98–Feb 99	53.4 [w-1]	11.6 [w-1]	103.3 [w-1]	–
T4 (north)	1	59	May 04–Apr 07	18.6 [n-4]	2.4 [n-5]	11.4 [n-4]	3.5 [n-2]
T5 (north)	1	31	Apr 05–Dec 05	15.1 [n-5]	5.2 [n-4]	6.5 [n-5]	–
T6 (north)	1	36	Apr 06–Apr 07	46.2 [n-1]	8.7 [n-1]	18.8 [n-2]	–
Captive-reared (north)	6	304	Dec 03–May 06	22.7	5.0	49.3	1.0
Female (north)	2	77	Feb 98–May 98	34.9 [n-1]	7.9 [n-1]	50.9 [n-1]	5.3 (*n*=1) [n-1]
Female (west)	3	117	Feb 98–Feb 99	42.4 [w-1]	11.2 [w-1]	88.6 [w-1]	6.6 (*n*=1) [w-1]
Male (north)	9	394	Oct 97–Apr 07	25.4 [n-2]	5.3 [n-2]	23.6 [n-2]	3.6 (*n*=6) [n-2]
Male (west)	5	203	Nov 97–Aug 99	34.9 [w-2]	8.1 [w-2]	41.5 [w-2]	6.2 (*n*=2) [w-2]
Hatch-year (north)	4	184	Oct 97–Feb 99	21.7 [n-3]	5.2 [n-2]	25.6 [n-2]	2.5 (*n*=4) [n-3]
Hatch-year (west)	2	67	Nov 97–Feb 99	32.5 [w-3]	5.8 [w-3]	52.2 [w-3]	–
Second-year (north)	3	106	Jan 98–Dec 05	33.6 [n-1]	8.0 [n-1]	40.8 [n-1]	7.9 (*n*=1) [n-1]
Second-year (west)	4	157	Feb 98–Jul 98	39.2 [w-2]	10.6 [w-1]	58.4 [w-2]	8.6 (*n*=2) [w-1]
After-second-year (north)	5	221	Feb 98–Apr 07	28.9 [n-2]	4.8 [n-3]	19.1 [n-3]	3.2 (*n*=3) [n-2]
After-second-year (west)	2	96	Feb 98–Aug 99	40.0 [w-1]	10.0 [w-2]	67.5 [w-1]	1.8 (*n*=1) [w-2]

western slope (too few western slope locations were generated during other translocation trials for comparison). Results of KDE and LCH methods were generally inconsistent in terms of how different age classes used the habitat, and results for 90% and 50% isopleths conflicted as well. The only area of agreement was that utilization distributions were largest for SY birds on the northern slope and smallest for HY birds on the western slope. The rank order of utilization distribution areas was relatively consistent between 90% and 50% isopleths using the KDE method. The LCH method produced a somewhat similar ranking for 90% isopleths, but there were too many missing values for 50% isopleths for comparison. Overall, the results indicated that control birds used large areas compared to translocated birds, translocated birds used relatively large areas during T6, T3, and T2, and captive-reared birds used areas that fell within the range of those estimated for translocated birds.

Results of data pooled from all individuals within categories of sex, age, and translocation trial (Table 2.9) did not consistently agree with the results of the individual evaluations in rank order, and values of the pooled analyses were much larger in magnitude. The pooled and individual assessments agreed most frequently in the rank order of age effects, both for KDE and LCH methods but mainly for the 90% isopleths. Whereas individual assessments generated rank orders of age classes that differed for the northern and western slope birds, the ranks were the same for both populations when the data were pooled. On both slopes, therefore, SY birds were associated with the largest areas of habitat use and HY birds were associated with the smallest areas for both KDE and LCH methods but only for the 90% isopleths. Nevertheless, the area used by SY birds on the northern slope under the individual assessment was only 33.6 ha, whereas it was 140.7 ha for SY birds on the western slope. The KDE method also ranked female and male habitat use similarly under individual and pooled assessments, with females again using larger areas and with both sexes using larger areas on the western slope. Results of the LCH method, on the other hand, were inconsistent. The rank orders of utilization distribution values for translocation trials were relatively consistent for both individual and pooled assessments but only for the LCH method and 90% isopleths. Areas used by T2 and T6 birds were the largest, and the size of areas used by captive-reared birds fell within the range of the values for translocated birds. The rank orders of values for seasonal use of habitat were relatively consistent for pooled assessments using both KDE and LCH methods and for 90% and 50% isopleths, especially for birds on the western slope. Areas used on the western slope were largest in spring and smallest in summer and fall, and areas used on the northern slope were larger in winter and smaller in summer.

After 21 days, the period when birds presumably had explored and become familiar with the reintroduction area, the 50% isopleth of the kernel density utilization distribution became smaller and less dispersed for 8 of 14 birds, while the 90% isopleth contracted for 7 birds. Additionally, we compared home range sizes of T1 and T2 birds during and after their first 20 days in the reintroduction area. The initial home range of T1 birds was markedly smaller than that of T2 birds and T1 home range size changed little over time (Figure 2.9). During T2, palila remaining on the northern slope for ≥21 days occupied a much larger home range in their first 20 days than they occupied later (Figure 2.9). Home range sizes of young birds (HY and SY) and mature birds (ASY) were similar during their first 20 days in the reintroduction area (t = 1.24, P = 0.27) and afterwards (t = 0.67, P = 0.52). Home range sizes of control palila on the western slope did not change over time.

Palila moved back-and-forth between the northern and western slopes, a distance of 16 km across inhospitable habitat (Banko *et al.* 2009). Following the translocation of 62 palila with

Table 2.9. The kernel density estimate (h = 150) and local convex hulls (k = 20 nearest neighbors) for categories of 90% and 50% utilization distributions (hectares) of palila. Rank order of kernel and hull estimates is shown in square brackets. Data from birds within each category were pooled, and observations of individuals were separated by at least one day to minimize spatial and temporal autocorrelation. Data for captive-reared birds were not used in sex, age, or other categories. Spring was defined as March, April, May; summer was June, July, August; fall was September, October, November; and winter was December, January, February.

				Kernel density estimates (ha)		Local convex hulls (ha)	
Category (slope)	Palila	No. obs.	Period	Mean 90%	Mean 50%	Mean 90%	Mean 50%
T1 (north)	23	221	Feb 97–Nov 97	78.4 [n-4]	8.7 [n-4]	51.7 [n-4]	2.0 [n-5]
T1 (west)	26	184	Feb 97–Jul 02	247.8 [w-1]	53.4 [w-1]	428.0 [w-1]	41.1 [w-2]
T2 (north)	23	471	Oct 97–May 98	113.5 [n-1]	17.8 [n-1]	165.0 [n-1]	2.8 [n-3]
T2 (west)	20	466	Oct 97–Aug 99	235.4 [w-2]	48.2 [w-2]	183.0 [w-3]	19.7 [w-3]
T3 (north)	4	108	Nov 98–Feb 99	46.5 [n-5]	5.3 [n-6]	46.7 [n-5]	1.8 [n-6]
T3 (west)	5	74	Dec 98–Feb 99	104.3 [w-3]	18.8 [w-3]	183.4 [w-2]	50.1 [w-1]
T4 (north)	15	115	Apr 04–Apr 07	37.9 [n-6]	8.4 [n-5]	17.5 [n-6]	2.7 [n-4]
T5 (north)	53	320	Mar 05–May 07	85.8 [n-2]	12.8 [n-3]	59.2 [n-3]	6.0 [n-2]
T6 (north)	27	210	Mar 06–Apr 07	82.0 [n-3]	14.0 [n-2]	112.0 [n-2]	6.9 [n-1]
Captive-reared (north)	14	372	Dec 03–Apr 07	81.2	13.7	51.7	1.7
Female (north)	61	588	Feb 97–May 07	135.6 [n-1]	20.0 [n-2]	112.0 [n-2]	5.5 [n-2]
Female (west)	23	312	Feb 97–May 06	299.3 [w-1]	68.0 [n-1]	238.5 [n-2]	50.6 [w-1]
Male (north)	75	760	Feb 97–Apr 07	133.7 [n-2]	23.2 [n-1]	172.9 [n-1]	6.8 [n-1]
Male (west)	29	409	Feb 97–May 06	250.3 [w-2]	49.2 [w-2]	368.5 [w-1]	25.1 [w-2]
Hatch-year (north)	12	270	Oct 97–May 06	71.6 [n-3]	10.5 [n-3]	88.8 [n-2]	2.5 [n-3]
Hatch-year (west)	11	207	Oct 97–Feb 99	158.0 [w-3]	32.5 [w-2]	215.2 [w-2]	21.9 [w-3]
Second-year (north)	67	609	Feb 97–Apr 07	140.7 [n-1]	17.8 [n-2]	150.5 [n-1]	5.2 [n-2]
Second-year (west)	35	372	Feb 97–May 06	288.3 [w-1]	63.6 [w-1]	333.0 [w-1]	39.9 [w-1]
After-second-year (north)	65	561	Feb 98–May 07	113.0 [n-2]	19.2 [n-1]	88.4 [n-3]	6.6 [n-1]
After-second-year (west)	11	165	Feb 98–May 06	161.8 [w-2]	32.1 [w-3]	191.8 [w-3]	30.6 [w-2]
Spring (north)	128	854	Mar 97–May 07	131.4 [n-2]	22.8 [n-1]	83.2 [n-2]	3.6 [n-3]
Spring (west)	39	321	Mar 97–May 06	329.7 [w-1]	69.8 [w-1]	445.3 [w-1]	56.1 [w-1]
Summer (north)	25	113	Jun 04–Aug 06	72.4 [n-4]	16.6 [n-4]	19.4 [n-4]	2.5 [n-4]
Summer (west)	10	124	Jun 97–Jul 02	102.2 [w-3]	22.3 [w-3]	140.9 [w-4]	7.6 [w-3]
Fall (north)	24	181	Oct 97–Nov 06	109.1 [n-3]	19.6 [n-2]	57.4 [n-3]	6.0 [n-2]
Fall (west)	8	23	Oct 97–Nov 02	63.7 [w-4]	14.1 [w-4]	329.2 [w-2]	–
Winter (north)	51	669	Feb 97–Feb 07	136.5 [n-1]	16.9 [n-3]	180.4 [n-1]	8.4 [n-1]
Winter (west)	31	280	Feb 97–Dec 02	231.9 [w-2]	52.3 [w-2]	325.0 [w-3]	34.7 [w-2]

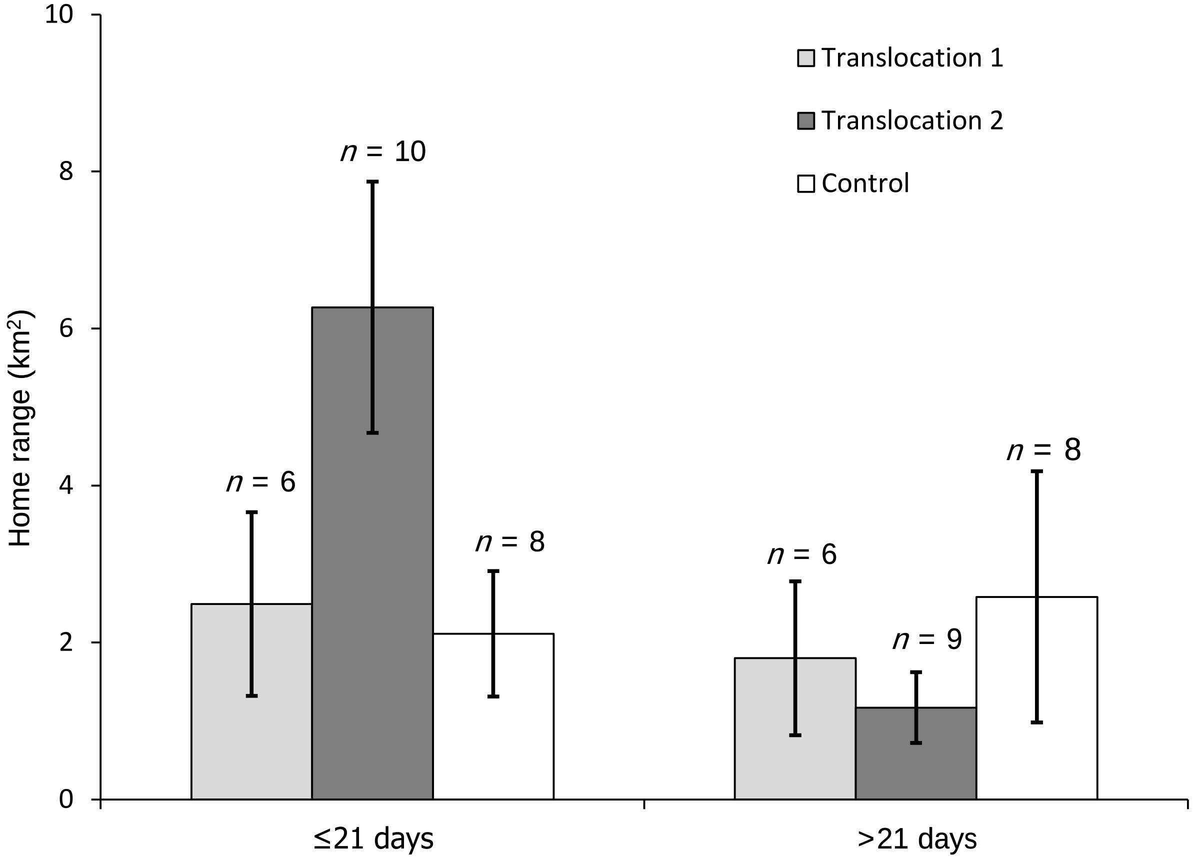


Figure 2.9. Change in home range size ≤21 days after release and >21 days after release for palila that were translocated or monitored as controls during T1 and T2.

radio transmitters during March–April 2005 (T5), we documented at least six palila commuting (moving back-and-forth) between the northern and western slopes. The 2005 commuting birds were three ASY males, one ASY female, and two SY females. Three birds made one known commuting trip (i.e., they were detected once on the western slope, then again on the northern slope), and were last detected on the north in May, July, and October 2005. Two other birds made two trips: returning to the western slope, coming back to the northern slope, and then making a second trip back to the western slope. The last bird traveled twice to the western slope and was last detected on the northern slope in June 2007. Seven additional T5 birds might have commuted, but uncertainties in the telemetry data prevent definitive conclusions. Additional support for commuting behavior comes from two birds from T4. These birds were not detected in the release area for five to six months during intensive monitoring, but they later reappeared and successfully bred on the northern slope in summer 2005.

We detected an unbanded ASY male on the northern slope in the summer of 2005 who had, evidently, immigrated from the western slope to the northern slope independently of translocation. We captured and radio-tagged him on the northern slope and then, less than two weeks later, tracked him to the western slope. Additional unbanded birds were detected on the northern slope into 2011 (Table 2.10).

Table 2.10. Demography of reintroduced palila colony on the northern slope of Mauna Kea, 2008–2012.

	2008[1]	2009	2010	2011	2012
Search effort (person-hours)	284	123	261	231	19
Translocated	4	2	1	0	0
Captive-reared[2]	2	2	2	1	0
F1 generation (banded)	3	0	0	0	0
Unbanded adults (minimum)	1	2	7	1	0
Unbanded fledglings (minimum)	2	1	4	0	0
Total number detected (minimum)	12	7	14	2	0

[1] Dates of surveys: 2008 (11–13 Mar; 10–12 Jun; 24–26 Sep); 2009 (3–5 Mar; 21–22 Jul); 2010 (13–16 Apr; 28 Jun–1 Jul; 7–9 Sep; 6–8 Dec); 2011 (8–9 Mar; 20–23 Jun; 26–29 Sep); 2012 (31 Jan–3 Feb).

[2] Releases of captive-reared birds by KBCC: Dec 2003 (10); Dec 2004 (5); Nov 2005 (6); Mar 2009 (7).

Roosting Behavior and Characteristics of Roost Sites

We found 161 night roosts on the northern slope of Mauna Kea in T2 (Figure 2.10) and T3 (n = 16 birds), and another 175 roosts on the western slope of returned or comparison palila (n = 16 birds) from November 1997–February 1999. We recorded 27 roost locations over 63 days for a SY female on the western slope during summer, the most recorded for any individual during T2.

The most roost locations identified for a T3 bird was the 32 we recorded over 65 days for a HY palila on the northern slope during the winter. Palila roosted solely in māmane trees on the northern slope (161 locations, 16 birds) with none roosting in naio, which was not abundant there. Māmane was used less often for roosting on the western slope, where naio was commonly available. Of 175 roost detections, 36% occurred in māmane, 57% occurred in naio, and 7% occurred in mixed naio-māmane clumps.

On the western slope, 11 of 16 birds roosted in both māmane and naio, two used only māmane, and three used only naio. There was a highly significant difference by slope in the species of tree used for roosting (χ^2 = 141.9, $P < 0.001$) likely due to the difference in forest diversity and tree availability (see below). Palila tended to roost more often in the same place each night on the western slope than they did on the northern slope (mean roost fidelity = 2.04 west, 1.49 north; range = 1.00–6.25 west, 1.00–2.36 north), but the difference was not significant (Mann-Whitney U = 70.5, P = 0.48). Palila usually roosted alone, but based upon instances when the observers were confident of detecting all the occupants in a roost tree, communal roosting occurred in 19 of 64 (30%) occasions on the northern slope and 15 of 64 (23%) occasions on the western slope. We were not able to identify roost mates or determine whether pairs of palila might have roosted together on some occasions.

No single factor (slope, age, sex) or interactions among factors (slope:age, slope:sex, age:sex) significantly explained differences in the distance between centers of diurnal utilization areas and night roosts during T2–T3 in a general linear model (Table 2.11; n = 29 birds, F = 0.62, overall P = 0.79). The difference between the 1032 m travelled on the western slope and the 658 m on the northern slope was the only parameter that was even marginally significant (P =

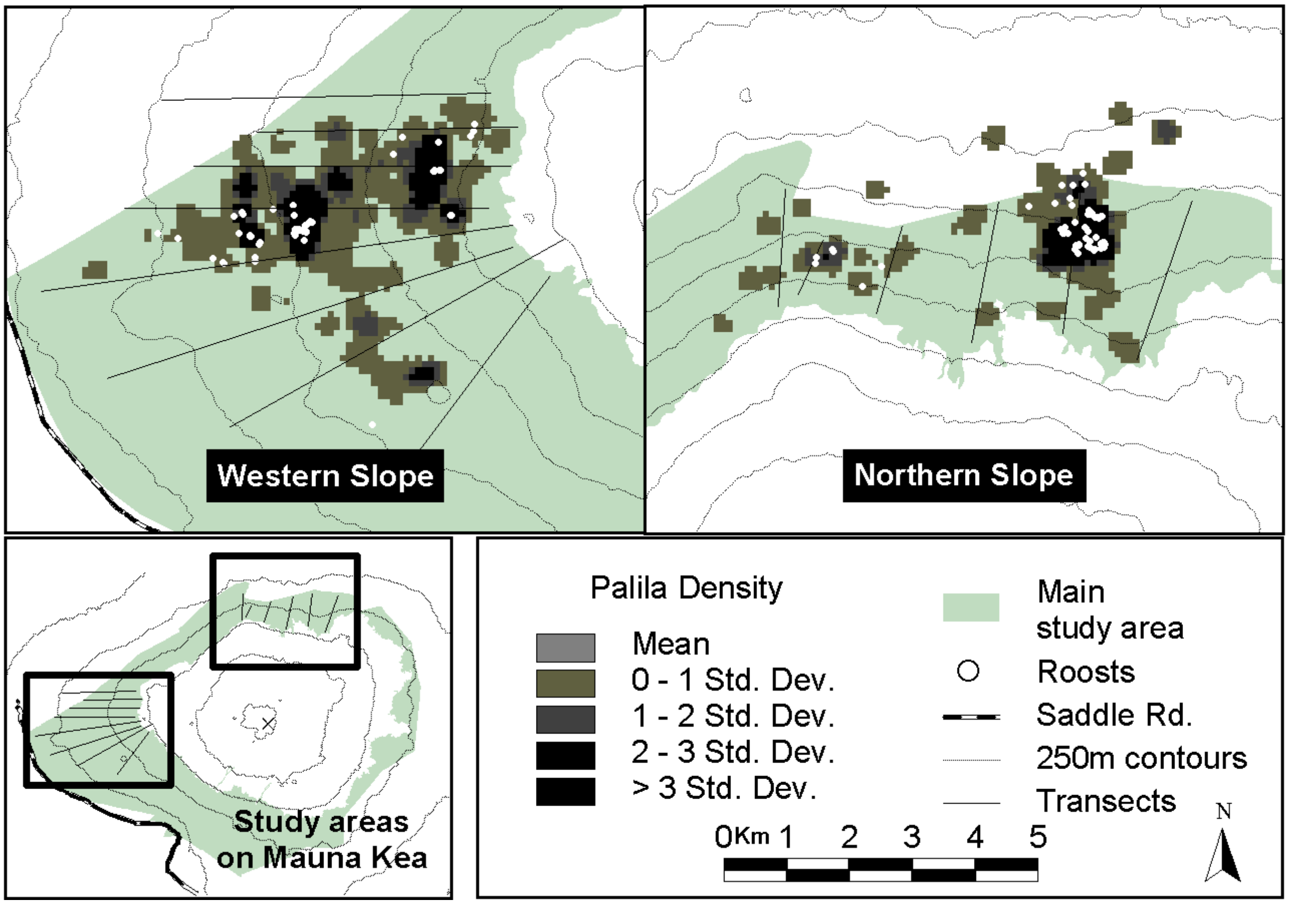


Figure 2.10. Roost locations and palila densities on the western and northern slopes of Mauna Kea during translocation 2.

0.09). Roosts were not clustered for those birds with multiple night roosts (12/14 northern slope birds; 12/12 western slope birds). Although night roosts of individual birds were not clustered, 84% of roosts on the northern slope fell within the 90% utilization distribution isopleths and 59% of roosts fell within the 50% isopleths (n = 9 birds); 84% of roosts on the western slope were located within the 90% isopleths and 64% were within the 50% isopleths (n = 6 birds).

None of the variables significantly distinguished between focal roost trees and paired trees, although canopy area and canopy overlap ranked highest for roost sites evaluated during T2–T3. Focal roost trees generally had larger canopies by area and volume and they had greater canopy overlap with adjacent trees than did the paired trees measured for comparison. Tree height (Table 2.12) and canopy area over the entire 0.04 ha plot also were identified with relatively high values in the discriminant analysis, but other characteristics of the trees, vegetation, or habitat within the plots failed to distinguish focal roost trees from paired trees.

Canopy cover was 51% around focal roost trees in the northern slope forest during T2–T3 compared to 6% in the forest at large, which was the only statistically significant difference when we compared forest structure immediately around focal roost trees to forest structure in

Table 2.11. Distance between night roost locations and daytime habitat utilization distribution centroids for individual birds in T2 and T3 (1997–1999). The uneven sample sizes were caused by two birds (HY unknown sex and SY female) that had sufficient day and night detections on both the northern and western slopes.

	Palila	Distance (m)
North	15	658
West	14	1032
Male	13	788
Female	9	747
Unknown	5	746
Hatch-year	9	607
Second-year	11	904
After-second-year	7	755

Table 2.12. Palila focal roost tree height (m) compared to paired trees and general subalpine forest on Mauna Kea. All roosts are the 236 roosts used by 32 birds during November 1997–February 1999, focal roosts (*n* = 30) and paired roosts (*n* = 30) are trees chosen for intensive vegetation sampling, and general subalpine forest is based upon the mean value from all 40 x 40 m vegetation plots within 750 m of the focal roost tree.

		Māmane	Naio	All
All roosts				
	north	3.5	–	3.5
	west	4.3	4.0	4.2
Focal roosts				
	north	6.2	5.2	6.1
	west	5.2	6.5	5.8
Paired roosts				
	north	6.0	4.8	5.9
	west	4.6	6.1	5.3
General forest				
	north	3.3	–	3.3
	west	4.8	3.9	4.2

vegetation plots within 750 m of focal roost trees in the three forest types (Table 2.13). Considering the comparisons individually, variables that significantly distinguished between roost sites and the forest generally were: the percent cover in the māmane-dominated forest (32% around focal roost trees, 12% in general forest; *P* = 0.0004) and stem density (225 around focal roost trees, 76 in general forest, *P* = 0.02).

We located 52 roosts of 18 palila during T4–T6, including seven locally produced F-1 generation juveniles. Contrary to roost selection on the northern slope during T2–T3 but similar to the pattern observed on the western slope, birds of T4–T6 roosted in some of the few naio available on the northern slope on 14 of 52 (46%) occasions and they roosted in māmane on 28 (54%) occasions. Likewise, these birds were more variable in selecting their roost species

Table 2.13. Forest structure measurements (mean ± SD) in 11.3-m radius plots around focal roost trees and in 40 x 40-m plots located within 750 m of the focal roost trees (see Chapter 25: Vegetation Survey in Palila Critical Habitat). To achieve an experiment-wise Type I error rate of 0.05, a Bonferroni-corrected *P*-value of 0.0028 was used as the threshold of significance. Sample sizes differed across comparisons because not all measurements were taken for all trees, nor were all survey methods used in all plots.

	Maximum height (m)	Canopy area per tree (m^2)	Stems/ha	% cover
Mixed forest				
roost area	5.7 ± 0.90 *n* = 10	22.1 ± 12.71 *n* = 10	470.0 ± 324.2 *n* = 10	48 ± 12.5 *n* = 10
forest	4.7 ± 0.47 *n* = 46	71.0 ± 38.38 *n* = 46	331.3 ± 201.7 *n* = 46	34 ± 17.7 *n* = 46
	t = 1.77, *P* = 0.0830	t = 1.38, *P* = 0.1727	t = 0.61, *P* = 0.5433	t = 0.83, *P* = 0.4094
Māmane forest				
roost area	4.4 ± 0.83 *n* = 10	17.4 ± 13.71 *n* = 10	152.5 ± 101 *n* = 10	32 ± 12.2 *n* = 10
forest	3.7 ± 0.67 *n* = 61	65.9 ± 32.77 *n* = 60	169.7 ± 87.1 *n* = 61	12 ± 9.1 *n* = 62
	t = 1.11, *P* = 0.2712	t = 1.57, *P* = 0.1216	t = 0.19, *P* = 0.8474	t = 2.06, *P* = 0.0434
North slope				
roost area	4.4 ± 0.82 *n* = 10	24.8 ± 11.95 *n* = 10	225 ± 87.4 *n* = 10	51 ± 18.4 *n* = 10
forest	3.3 ± 0.80 *n* = 19	69.1 ± 56.78 *n* = 19	75.7 ± 43.1 *n* = 19	6 ± 6.1 *n* = 21
	t = 1.39, *P* = 0.1769	t = 0.94, *P* = 0.3536	t = 2.43, *P* = 0.0222	t = 3.97, *P* = 0.0004

compared to the T2–T3 birds. Seven (39%) birds roosted both in naio and māmane, two (11%) exclusively used naio, and the remaining nine (50%) exclusively used māmane. The seven locally produced birds were similar to the reintroduced population as a whole: three birds roosted in both tree species, one used only naio, and three used only māmane. The data also indicated lower roost fidelity of T4–T6 birds (mean = 1.09, range 1.0–2.0, *n* = 18 birds) compared to T2–T3 birds. Additionally, communal roosting (up to eight birds in the same tree) more than doubled during T4–T6: 63% (33/52) of observations were of multiple birds in the same tree and 37% (19/52) were of single palila. Six locally produced birds roosted with other palila on 68% (17/25) of occasions compared to 59% (16/27) for other palila. Although none of the locally produced palila was observed roosting with a sibling, two roosted with a parent: one with its mother on three of five occasions and the other with its father on one occasion.

Reproduction Within the Reintroduced Colony

We attempted to create a balanced sex ratio in the reintroduced population, but our effectiveness was limited by low capture rates and a strong male bias in the source population on the western slope (see Chapter 6: Sex Ratio). During the first translocation, when we moved only SY palila, breeding was not expected because SY males do not breed (Pratt *et al.* 1997). The sex distribution of breeding-age palila was nearly even in T2, but males greatly outnumbered females in T4 and T6 and females greatly outnumbered males in T5 (Figure 2.3). Based on plumage characteristics (Jeffrey *et al.* 1993), the sex ratio of birds released during T4–T6 was close to even (60F:67M; Table 2.3). The ratio of breeding-aged females to males was nearly even (59F:62M) over the entire span of T4−T6, when many mature palila were translocated in hopes of stimulating reproduction. However, the annual operational sex ratio of the northern slope colony changed frequently due to emigration, death, or additional releases, such that during the primary breeding months of April–July the operative sex ratio was moderately male-biased overall (mean = 43% F), ranging from female-biased (31F:20M [61% F]) in 2005 to strongly male-biased (13F:27M [33% F]) in 2006.

We did not intentionally translocate paired or breeding palila. Nevertheless, we captured adult males and females in the same net within 15 minutes of one another on two occasions during both T1 and T2 and on 11 occasions during T4 and T5, indicating that they may have been paired at the time. No breeding was observed during 1997−1999 (T1−T3), when most translocated males were immature, but we detected reproduction in the reintroduction area every year during 2004–2010 (T4−T6). Of 135 palila translocated during T4–T6, at least 16% (10 F, 11 M) established pair-bonds and 13% (9 F, 8 M) nested in the reintroduction area during 2004–2007, when our intensive monitoring was more likely to detect reproductive behavior. Among the 59 birds that remained eight weeks or more in the reintroduction area during T4−T6, at least 29% nested. Of the 28 captive-reared birds released into the reintroduction area, five (2 F, 3 M) attempted to breed during 2004−2009. Pair bonds were formed among and between translocated and captive-reared palila in the following combinations: translocated males paired with translocated and F1-generation females but not with captive-reared females; translocated females paired with translocated and captive-reared males; captive-reared males paired with captive-reared, translocated, or F1-generation females; captive-reared females paired exclusively with captive-reared males.

During the period of intensive monitoring (2004–2007), we discovered four inactive nests (three empty, one with a dead chick), and twelve active nests, three of which fledged chicks (Table 2.14). We also detected six families (at least one adult, at least one fledgling) that were not associated with nests. Of egg-producing pairs, eight consisted only of translocated birds (9 F, 8 M), three consisted of translocated females (3) and captive-reared males (2), and two consisted only of captive-reared birds (2 F, 2 M). Over the four-year period, these 13 pairs produced at least 18 clutches, 27 eggs (1.5/clutch), 16 nestlings (0.89/clutch), and 11 fledglings (0.61/clutch). Although no eggs were hatched by captive-reared females, three fledglings resulted from two of the seven breeding attempts by captive-reared males that were mated with translocated females.

In 2008, despite reduced search effort, we located at least two palila families in the reintroduction area. One family was particularly noteworthy because the fledgling represented the F2 generation; its mother was a F1 offspring of translocated parents, its father was a translocated male, and it was being fed by both parents. The other family consisted of a fledgling that was fed by a captive-reared male; the mother was not observed but would have been either translocated or locally produced because no captive-reared females were present on the northern slope at that time. A fledgling accompanied by a translocated male likely represented a third successful breeding attempt in 2008, but we did not observe the male feeding the fledgling on the only occasion when they were seen together so we could not rule

Table 2.14. Reproductive effort of translocated, captive-reared, and F1 generation palila in the reintroduction area, 2004–2010.

Year	Female	Male	Pair-bond/nest	Egg/nestling	Fledgling
2004	T4-59[a]	T4-70		2 nestlings	
2004	C3.25[b]	C3.36		1 egg (infertile)	
2005	T5-19	T5-100	pair-bond		
2005	T5-61	T5-53		2 eggs (hatch, no hatch)	P1
2005	T4-06	C3.38		2 eggs (hatch)	P2, P3 (died)
2006	T5-19	T5-64		1 egg (hatch)	P4
2006	T6-24	T5-61			P5
2006	T5-52	T5-51			P6 (pair-bond)
2006	T5-52	T5-51, (T4-55[e])	(nest helper?)		P7
2006	T5-85	T4-55			P8 (pair-bond)
2006	T5-85	T4-55			P9, P10 (breed)
2006	T5-85	T4-55		1 egg (infertile)	
2006	T5-85	T4-55	nest (empty)		
2006	T5-150	T5-100		2 eggs (broken)	
2006	T5-666	T5-01	pair-bond		
2006	T5-92	C3.38		1 egg (broken)	
2006	T5-92	C3.38	nest (empty)		
2006	C4.48	C3.44	nest (empty)		
2006	C4.48	C3.44		2 eggs (fertile)	
2006	?[c]	?		inactive nest; 1 nestling (dead)	
2007	T5-52	T5-01		2 nestlings (died)	
2007	T5-150	T6-16	pair-bond		
2007	T5-19	C3.44			P11
2007	T5-19	C3.44		1 egg, 1 nestling (disappeared)	
2007	T5-92	C3.38		2 eggs (broken)	
2007	P6[d]	T6-14	pair-bond		
2007	P8	C5.55	pair-bond		
2007	P10	T6-36	pair-bond		
2008	P8	T6-16	pair-bond		
2008	P10	T5-01			P12 (F2 generation)
2008	?	T6-14			P13[f]
2008	?	C3.44			P14
2009	?	C3.44			P15
2010	?	?			P16[f]
2010	?	?			P17[f]
2010	?	?			P18[f], P19[f]

[a] T4-59 = wild bird (T)ranslocated in 200(4), bird #(59)

[b] C3.25 = (C)aptive-reared bird released in 200(3); bird #(25)

[c] ? = bird not observed; identity and origin unknown

[d] P6was a generation F1 fledgling that was produced in reintroduction area by a translocated, captive-reared, or other F1 generation bird.

[e] T4-55 was observed feeding fledgling P7, suggesting that he was a nest helper.

[f] Fledgling was not observed being fed by associated adult, but was assumed to be its offspring.

out the possibility that they were fortuitously associated due to local food availability or social attraction.

The same captive-reared male that was tending a fledgling in 2008 was again observed feeding a fledgling in 2009, but we could not identify his mate. This male sired at least three fledglings, making him the most prolific captive-reared palila.

In September 2010, at least four fledglings in three family groups were observed near Pu'u Mali. All fledglings were associated with unbanded birds, suggesting that breeding was occurring among the unbanded descendants of translocated pairs or pairs of mixed origin (i.e., translocation and captive-rearing). Therefore, during 2004–2010, we observed a total of 19 fledglings in 16 families (Table 2.14).

Relatively few palila nested in the reintroduction area overall, but those that nested successfully also tended to nest in multiple years or multiple times during a single season. A total of 49 mature females, including 9 captive-reared females were available to breed in the reintroduction area during at least a portion of the spring and summer (April−July) of 2004–2007. Of these, four translocated females (44%) produced more than one fledgling each, or 82% (9/11) of all fledglings, while two other translocated females produced the remaining two fledglings. Two translocated and one captive-reared male presumably sired 64% (7/11) of the fledglings, and three other translocated males and a captive-reared bird sired the remaining four fledglings.

The number of fledglings produced per available female increased in each year during 2004–2006 but declined in 2007. In 2004, one of seven females nested, but no fledglings were produced, although two nestlings survived nearly to the expected time of fledging. In 2005, 2 of 24 females nested and produced three fledglings (0.12/female). In 2006, 7 of 14 females nested and produced seven fledglings (0.5/female). In 2007, three of four females nested and produced one fledgling (0.25/female). Of the 11 total fledglings produced, 10 survived through their four-month period of dependency on parental care and 8 survived to maturity (Table 2.15).

Table 2.15. Survival times and breeding status of palila fledglings in the reintroduction area.

Year	Fledgling	Band	First detection	Last detection	Survival (day)	Survival (month)	Breeding status
2006	P9[a]	805102988	28-May-06	29-Jun-06	32	1.1	
2005	P3	unbanded	27-Jun-05	12-Oct-05	107	3.6	
2005	P2	88159480	27-Jun-05	1-Nov-05	127	4.2	
2005	P1	88159479	5-Jul-05	23-Feb-06	233	7.8	
2006	P7	805102989	25-Jun-06	11-Apr-07	290	9.7	
2006	P4	805102991	4-Jul-06	4-Jul-07	365	12.2	
2006	P5	805102992	29-Jul-06	17-Oct-07	445	14.8	
2007	P11	805102993	8-Jun-07	25-Sep-08	475	15.8	
2006	P6	805102986	13-Apr-06	13-Mar-08	700	23.3	pair bond
2006	P10	805102990	25-Jun-06	25-Sep-08	823	27.4	nested
2006	P8	805102987	13-Apr-06	25-Sep-08	896	29.9	pair bond

[a] P9 was abandoned by its parents and was fed by a Hawai'i 'amakihi (*Hemignathus virens*; Farmer *et al.* 2008).

Long-term Persistence in the Reintroduction Area

The rate of attrition of translocated palila was initially rapid before slowing greatly after about 90 days (Figure 2.11), but there were no differences attributable to age or sex (Figure 2.12). The daily rate at which birds (*n* = 168) were lost from the reintroduction area was 1.5% during days 1–89 and 0.27% during days 90–730. Including all 188 translocated birds, 21 (11%) of the 188 translocated palila and at least one from every trial except T3 were detected in the reintroduction area over a period of 12 months or longer (>362 days) after being translocated (Table 2.16). Nevertheless, lengthy gaps in detection frequency suggested that some birds may have intermittently traveled to the western slope or elsewhere, although none of the 21 palila was observed moving between the two areas. The birds most likely to have traveled at some time during their tenure on the northern slope were seven individuals with gaps in detection lasting at least six months. The longest gap was 34.4 months, when a T6 female that had not been observed on the northern slope since June 2007 reappeared there in April 2010, four years after being translocated. The mean (± SE) gap in detecting the 20 other palila was 4.5 ± 0.67 months (range = 1.3–13.2). Highly persistent birds equally consisted of males (*n* = 10) and females (*n* = 11). When translocated, eight of the females were SY and three were ASY, whereas nine of the males were ASY and one was HY (Table 2.17). At least six locally produced offspring survived and remained in the reintroduction area for a year or longer. Nevertheless, following the last translocation, the northern population declined to low numbers due to emigration or mortality (Figure 2.13).

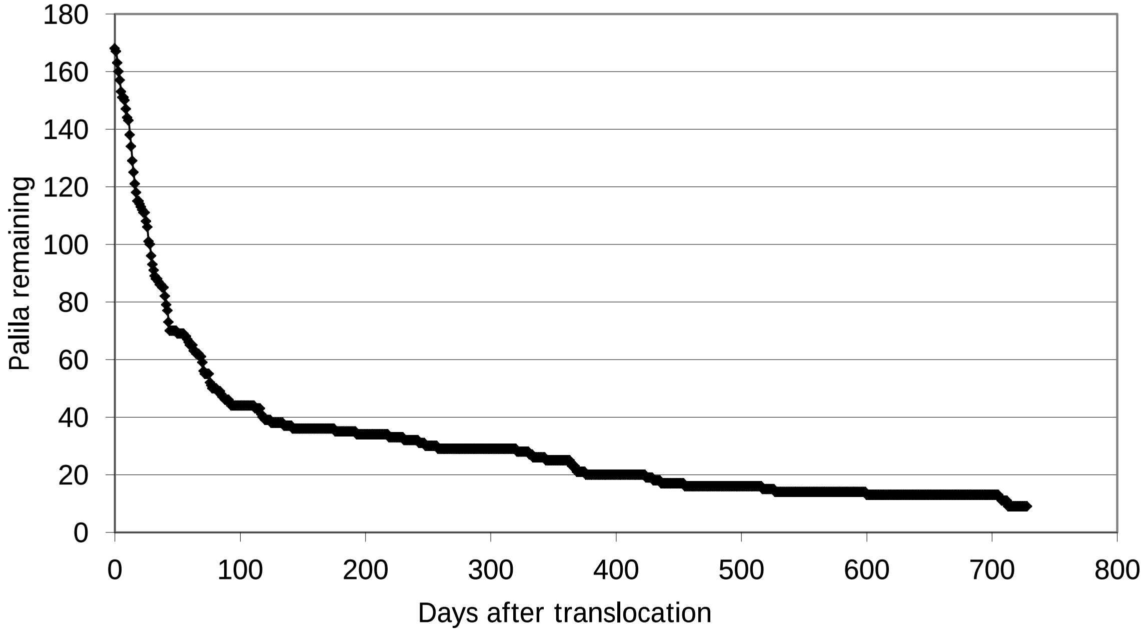


Figure 2.11. Rate of attrition of palila (*n* = 168) translocated to the northern slope of Mauna Kea, 1997–2006. The daily rate at which birds were lost from the reintroduction area was 1.5% during day 1–89 and 0.27% during day 90–730. Twenty-one (13%) remained one year or more.

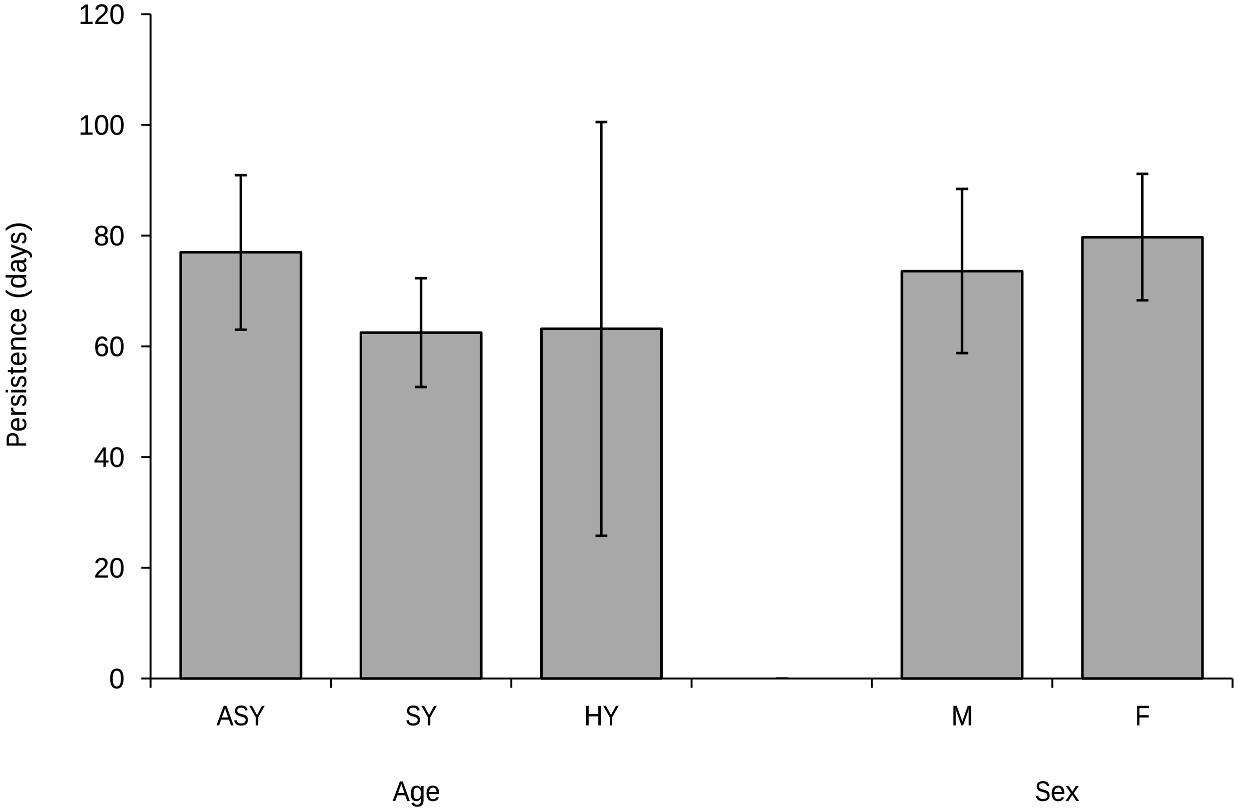


Figure 2.12. Persistence of translocated palila in the reintroduction area during T1–T5, by age (ASY = after second year, SY = second year, HY = hatch year) and sex.

When intensive surveys ended in August 2007, at least 21 palila remained on the northern slope: 12 translocated birds from T4–T6, 3 captive-reared birds, and 6 locally produced offspring (F1 generation). Results of subsequent surveys, involving about 15% of the previous search effort and conducted at two-to-four-month intervals, indicated a decline of translocated birds from four in 2008 to one in 2010 and the disappearance of the six banded F1-generation birds. No translocated birds were detected after 2010. Two captive-reared palila persisted into 2010, but only one remained in 2011 and none were seen afterward. On the other hand, more unbanded adults (origin unknown) and fledglings were observed on the northern slope in 2010 than were detected there in 2008 and 2009 combined. Nevertheless, no palila were detected in the reintroduction area after mid-2011 (last survey in February 2012).

Discussion

Capture Rates

Palila capture rates were similar during the first three translocations, but we caught birds at much lower rates during T4–T6 (Table 2.1). Capture rates were perhaps lower during the early breeding season, when T4–T6 birds were netted, as birds focused on breeding activities near their nesting sites. We began netting earlier in the year during T5 and T6, and our capture rate increased somewhat possibly because we captured females before they started nesting.

Table 2.16. Translocated palila persisting in the reintroduction area for 12 months or longer (>362 days).

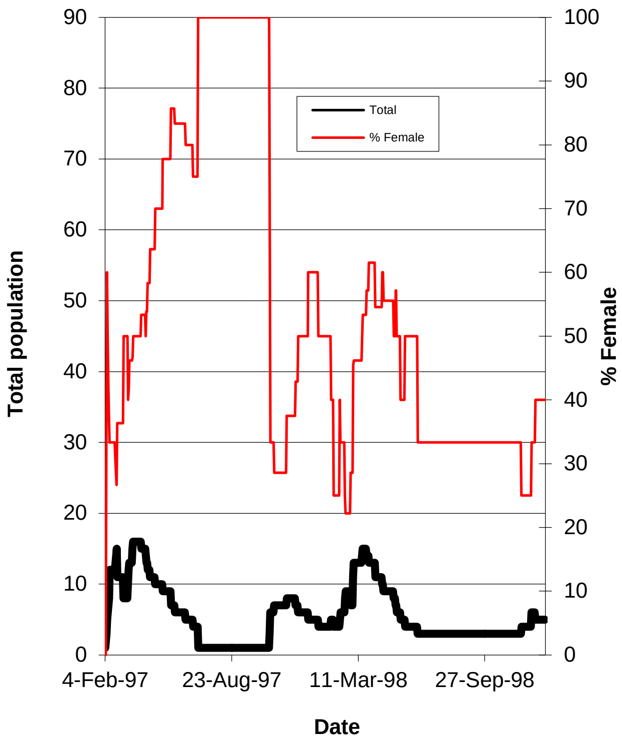
Bird	Sex	Age	Translocation date	Maximum days on north	Maximum detection gap (days)	Maximum detection gap (months)
T1-34	F	SY	20-Mar-97	363	181	6
T2-02	M	HY	22-Oct-97	454	116	3.8
T4-06	F	ASY	10-Apr-04	516	227	7.5
T4-55	M	ASY	28-Apr-04	1129	186	6.1
T5-666	F	SY	24-Apr-05	364	55	1.8
T5-475	F	SY	25-Apr-05	429	118	3.9
T5-100	M	ASY	22-Apr-05	599	91	3
T5-85	F	SY	21-Apr-05	707	71	2.3
T5-64	M	ASY	17-Mar-05	712	61	2
T5-51	M	ASY	14-Apr-05	728	64	2.1
T5-61	F	ASY	17-Mar-05	812	162	5.3
T5-52	F	ASY	14-Apr-05	845	102	3.4
T5-92	F	SY	23-Apr-05	851	58	1.9
T5-150	F	SY	27-Apr-05	904	89	2.9
T5-01	M	ASY	16-Mar-05	1289	236	7.8
T5-19	F	SY	25-Apr-05	1444	400	13.2
T6-36	M	ASY	25-Apr-06	435	40	1.3
T6-04	M	ASY	14-Mar-06	526	63	2.1
T6-16	M	ASY	9-Apr-06	712	155	5.1
T6-14	M	ASY	7-Apr-06	1083	267	8.8
T6-24	F	SY	10-Apr-06	1468	1045	34.4

Table 2.17. Age and sex distribution of translocated palila persisting a year or more in the reintroduction area.

	HY	SY	ASY	Total
F	0	8	3	11
M	1	0	9	10
Total	1	8	12	21

Additionally, moving at least some net locations each day may have decreased habituation to nets by palila. Although capture rates for T1–T3 were similar, the number of palila caught per bird translocated was much higher for T3 because hatch-year birds were uncommon and scattered.

(A)



(B)

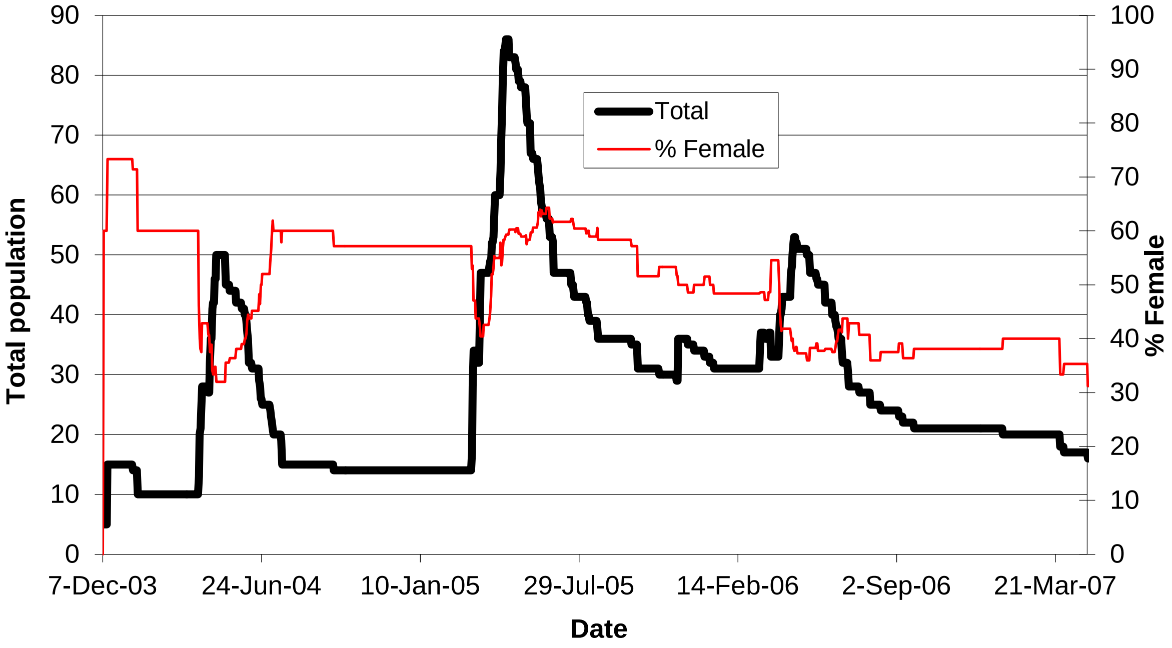


Figure 2.13. Changes in population size and proportion of female palila on the northern slope of Mauna Kea during (A) T1–T3 and (B) T4–T6 due to translocations of birds, emigration from the restoration site, mortality, and recruitment of young.

Health and Behavior of Translocated Palila

Few birds died soon after transport, leading us to conclude that our protocols were safe and generally suitable for transporting palila and perhaps other species. Nevertheless, transport by helicopter might be less stressful for birds when holding and transport on rough roads would exceed seven to eight hours.

Palila lost weight during transport, possibly because their metabolic rate increased due to stress. We found that both sexes and birds of all ages and sizes, based on wing chord or tarsus, lost the same proportion of body weight during transport, suggesting that palila responded universally to transport stress. Likewise, there was no effect of number of birds translocated on weight loss.

Many birds ate māmane flower parts and seeds during transport, but we did not detect a relationship between weight change and the amount of food eaten. Palila lost less weight during T4−T6 even though their average transport time then was nearly twice as long as it was in the earlier translocations. This may have been because we did not transport T4−T6 birds immediately after capture, as we did during T1−T3. Instead, we allowed birds to become calm for 0.25–4 hours prior to transport by holding them in individual, covered cages placed in shaded, quiet locations and we provided them with ample food. We were very cautious about not moving birds that seemed stressed in all trials, and most of the birds were generally calm during transport. We do not know whether the fluids we administered to some birds during T4−T6 alleviated some of the stress induced by holding and transport, but none seemed to suffer ill effects from this treatment. Different protocols might be required when transporting birds to more remote areas or when having to hold birds for more than eight hours.

Estimates of urate levels in feces produced ambiguous results that we found unhelpful in determining the level of stress experienced by translocated birds. Behavioral observations alone seemed adequate for deciding whether birds were unsuitable candidates for transport.

Monitoring

We invested a great amount of time in monitoring the reintroduced birds at the expense of capturing and transporting more birds. Nevertheless, we found that monitoring was critically important to evaluating the ultimate success of the translocation trials and reintroduction of captive-reared birds, and it was essential to understanding the factors affecting the survival and behavior of the birds. We gained new insights from each translocation trial and each release of captive-reared cohorts.

Radio transmitters were essential to a regular program of monitoring, but there were associated risks to the birds from the transmitter antenna becoming entangled (Dougill *et al.* 2000). Following problems with entanglement during T2, we switched to a different model transmitter, but even then some birds became entangled in T4. Although our intensive tracking schedule may have afforded us more opportunities to observe problems than might have been the case in studies in which birds fitted with the same style transmitters were observed less frequently, antenna entanglement in bark and twigs is a potential risk for birds that move over rough bark and among twigs and foliage when foraging (Jackson *et al.* 1977). Palila were entangled in a variety of ways in tree species that differed structurally, but they are probably less prone to entanglement than birds that creep close to the surface of branches or hang upside down. Intensive monitoring allowed us to rescue entangled palila in some cases. Design features that probably contributed most to entanglement were: excessive solder on the tip of the antenna (when not sheathed in plastic), excessive antenna length, and a limp antenna that dragged along the surface of branches. We also found that transmitters attached to birds with a harness did not fall off prematurely whereas transmitters that were glued on frequently fell off, such as in T4 when seven glue-on transmitters fell off after 24.6 ± 23.4 days (range = 1–54 days). The glue-on technique might produce variable results depending on variation in the shelf-life and formulation of different batches of glue.

Short-term Fates and Persistence Times of Reintroduced Birds

Using both radio-tracking and re-sighting observations allowed us to determine the eight-week fate of 15 additional translocated birds for a total of 121. This improvement led us to conclude that short-term persistence in the release area was 34% rather than only 25% because while radio-tracking target birds we occasionally encountered additional birds whose radios had failed but whose leg bands allowed us to identify them. Additionally, palila were relatively conspicuous in the limited amount of suitable habitat available on the northern slope, and radio telemetry was not always required to find individuals.

Emigration was more difficult to estimate because returning birds were seldom identified by re-sighting (n = 21) or re-capture (n = 15) in the large western slope area. Re-sighting added only one bird to the list of emigrants (20–21%) detected by radio-tracking; consequently, emigration was likely to have been underestimated overall (i.e., many birds whose fates were undetermined could have emigrated). Estimates of emigration during each of the translocation trials also could have been affected by variation in monitoring effort on the western slope and by the five-year gap between T3 and T4. During T1–T4, we regularly searched for control birds on the western slope and so had more opportunities to detect emigrants. We also had more opportunities for detecting emigrants during the five-year gap between T3 and T4 when we conducted other studies of palila ecology on the western slope. During T5 and T6, when controls were not used, we monitored birds primarily on the northern slope and so had fewer opportunities to detect emigrants on the western slope. Due to disparities in geographical area and monitoring effort, therefore, it seems likely that emigration rates of T5–T6 birds were underestimated, even considering that emigration overall was probably underestimated.

The frequency at which birds returned to the western slope indicated that the 16-km distance separating capture and release sites did little to impede movement around the mountain. At least four birds emigrated within a week of being translocated, suggesting that they might have been separated from mates when they were captured, whereas 69% (24/35) of emigrants stayed on the northern slope at least one week. Using all possible data from the six translocations, emigrants remained on the northern slope 11 days before returning to the western slope, and they frequented habitat patches where other palila were generally found. Given that most birds remained in the reintroduction area for at least a week, it seems unlikely that holding birds in aviaries for days or weeks prior to releasing them would have increased their persistence. Moreover, our results indicated that about 34% of birds translocated during March−April, just before the main breeding season, remained in the reintroduction area long enough to have an opportunity to breed.

Sex, age, and other factors did not predict the persistence time of translocated palila, and our study design did not allow us to test for the effects of season because most birds were translocated shortly before the primary breeding season. During T1−T3, we attempted to translocate young (HY, SY) birds under the assumption that their site fidelity would have been weakly developed, but our sample of HY birds was limited (n = 12) and even then probably included birds older than six months. There was a very short period for targeting juveniles that were very young as well as independent of parental care, and such juveniles were not abundant in the general population due to low recruitment in most years (see Chapter 9: Breeding Phenology, Productivity, and Nesting Success). The SY birds and the older HY birds, therefore, may already have developed some affinity to their natal area on the western slope. Alternatively, or in addition, juveniles as well as adults may have returned to the western slope soon after translocation because of strong social attractions. Adults may have been inadvertently separated from their mates, and juveniles might still have been socially associated with their families or even with other independent juveniles. Juvenile palila are dependent on adult care for up to four months, and some receive assistance from adult male relatives other than their fathers (Miller 1998, Patch-Highfill 2008). Additionally, juvenile palila engage socially to some extent with other palila after becoming independent of parental care (Miller 1998). Although our knowledge of palila social systems is limited (Pratt *et. al.* 1997), these and other social attractions may have stimulated some palila to return to the western slope. Social interactions may also have influenced the persistence of palila on the northern slope to some degree. Sociality might partially explain the nominally longer persistence of palila in T5, when we moved the most birds, regardless of sex or age. On the other hand, resident birds seemed not to influence the behavior of newly released individuals because persistence did not increase with successive translocation trials and birds that were translocated later did not persist longer than birds that were moved earlier during the same trial.

More translocated than control palila died, and mortality was due primarily to predation and transmitter entanglement (Dougill *et al.* 2000), which were implicated in the deaths of 14 birds on the northern slope during T2. Additionally, estimates of both emigration and persistence were likely reduced by the loss of the T2 birds. No translocated birds died during T1 or T3, and deaths in T4 were most likely not due to predators, suggesting that predator threats vary annually or seasonally. Although anomalous, the high (58%) loss of birds in T2 underscores the importance of effective predator control in re-introduction areas, where the vulnerability of translocated birds due to their unfamiliarity with the environment can be compounded by faulty monitoring equipment or other factors.

Habitat Utilization, Home Range, and Movement Between Western and Northern Slopes

Translocated palila explored the reintroduction area broadly, including sparsely wooded pasturelands below the forest reserve, but they gravitated to the densest stands of māmane soon after release and inhabited these areas almost exclusively thereafter. Captive-reared birds also primarily frequented the major māmane stands. Nearly all translocated palila centered their activity on the largest māmane stand located directly upslope from Pu'u Mali, but a few birds spent most of their time and nested in the two smaller stands that were located about 2.5 km to the west and across the pūkiawe shrubland.

Utilization distributions of individuals overlapped extensively, which was unsurprising given the absence of territoriality in palila (Fancy *et al.* 1993) and the limited amount (<100 ha) of prime habitat available on the northern slope. Individual and pooled assessments of habitat utilization distributions using KDE or LCH methods and 90% or 50% isopleths generated results that often conflicted in rank order and magnitude of the values. The most consistent results indicated that control birds on the western slope used larger areas than translocated or captive-reared birds on the northern slope and that females used larger areas than males. The larger utilization distributions of birds on the western slope were presumably due to the much more limited availability of habitat on the northern slope and the consistent use there of the largest habitat patch by nearly all birds. Females might forage over larger areas than males because their slightly smaller size may constrain their ability to detach and open māmane pods, which are tough even when green. The degree to which SY birds may also use larger areas of habitat could reflect their need to search for mates.

Our analyses of 95% kernel estimates revealed that home ranges of T1 birds did not change in size over time whereas home ranges of T2 birds were initially quite large before contracting after 20 days. Alternatively, initial home ranges may have been underestimated during T1 because monitoring efforts were reduced and locations were often difficult to obtain because birds moved frequently and far during the exploratory phase. The degree of home range contraction over time was not affected by bird age, suggesting that movement and habitat use patterns of young and older palila were generally similar. In addition, translocated palila that remained over 20 days tended to occupy somewhat larger home ranges than did birds that emigrated sooner, although the difference was not significant. Birds that were quick to return to the western slope, therefore, may not have explored the northern slope as thoroughly as did birds that remained longer in the reintroduction area.

Home ranges of control palila on the western slope were similar in size overall to those of translocated birds. Although home range size remained relatively constant over time, control birds shifted the center of their home ranges. This suggests that palila on the western slope utilized different areas throughout the monitoring period. In contrast, translocated palila tended to occupy the largest stand of māmane after their initial exploration of the larger region. As gaps among the few dense stands of māmane fill in with trees, the carrying capacity of the reintroduction area will increase considerably, enabling more birds to sustain themselves throughout the year.

An unexpected result of the translocation trials was that some birds occasionally traveled back and forth between the northern and western slopes. Understanding the basis for this commuting behavior could facilitate meta-population management to link subpopulations around Mauna Kea and perhaps eventually on Mauna Loa. Given that the reintroduced colony persisted for only five years after the last translocation, we cannot know whether or how gene flow between subpopulations might have been facilitated by palila that commuted between slopes. The two T4 birds that returned to the northern slope and nested, presumably after living for many months on the western slope, demonstrate one mode of gene flow. It is unknown whether unmarked palila that appeared on the northern slope in the last few years knew of its existence, were somehow influenced by the behavior of commuters, or were simply exploring far from home. Neither do we know how movement between areas may be affected by habitat conditions at the reintroduction area, the source area, and the region between them. However knowledge of alternative habitat may be acquired, the long-distance movement of birds around Mauna Kea could prove to be an important hedge against adversity on the western slope. Additionally, the social environment may influence palila movements, despite inconclusive results in our study. Additional studies might reveal how the size and composition of the population in the reintroduction area affects the responses of newly translocated birds.

Related to the commuting behavior of translocated birds was natural immigration of wild palila. Although there is no evidence of a resident population on the northern slope of Mauna Kea since 1965 (Walker 1968), we documented wild palila at least occasionally appearing there. Having caught one such immigrant and radio-tracked it to the western slope, it seems likely that other natural immigrants also originated there, especially as it is home to nearly all palila.

The rate of natural movement between slopes cannot be estimated with our data, but it may be relatively high because analyses of eastern and western slope palila indicated no genetic differentiation (Fleischer *et al.* 1994). A question for future research is whether natural immigration increases in frequency and duration as the palila population and habitat expand on the northern slope.

Roosting Behavior and Characteristics of Roost Sites

Our study of palila roosting behavior was unique in that most studies of roosting behavior have focused on the behavior of communally roosting birds and the information center hypothesis (Caccamise and Morrison 1988, Stouffer and Caccamise 1991). Only a few studies have been conducted on the roosting behavior of species that are solitary or non-territorial (Chandler *et al.* 1995). Fancy *et al.* (1993) concluded that palila did not regularly re-use roosts during their 1991 study of site tenacity, but they used radio triangulation to determine roost sites, and their error rates were large (160 ± 40 m). They concluded that palila did not return to a particular portion of their home range each night to roost. We found that palila roosted frequently in the same areas and even in the same trees. For example, one individual returned to the same tree for almost a month.

On the western slope, where both naio and māmane trees were abundant, palila more frequently roosted in naio. The availability of naio for roosting on the northern slope was limited to relatively few trees, and though the generally younger T2–T3 palila roosted only in māmane, the older birds of T4–T6 roosted in naio on 46% of occasions. There was no clear pattern of fidelity to individual roost trees, but the T4–T6 palila were more variable in terms of selecting roost tree species, exhibited lower roost fidelity, and roosted communally more frequently. Variables that distinguished roost sites from trees in the surrounding forest were higher tree and stem density.

Some birds used the same tree for consecutive nights and some individuals even used the same branch over multiple nights and weeks. Although some individuals roosted repeatedly in the same tree, most birds occasionally switched trees within a small area. Repeated use of roost trees may increase the vulnerability of palila to mammalian predators that use olfactory cues while hunting. Additionally, rats frequently forage in naio (Amarasekare 1994), where they may prey on roosting palila. Frequent shifting of roosts can limit both the visual and olfactory cues of fecal accumulations that may attract predators (Hughes *et al.* 2010). This hypothesis is worth examining for palila, because they tend to roost solitarily and do not have communal or other defenses against introduced mammalian predators. Additional studies of roosting behavior may help develop other aspects of predator management strategies and translocation techniques.

Demography, Reproduction, and Long-term Persistence

Numbers of palila on the northern slope fluctuated greatly during our translocation trials but fell within the range of population density found on the western slope (Banko *et al.* 2013) in the habitat patches that they frequented most often. This might suggest that the translocation site was saturated with palila and that more might have stayed had more or better habitat been available. Based on DNA, the sex ratio of translocated birds was male-biased but generally representative of the western population (Lindsey *et al.* 1995). The persistence and survival of translocated males and females were similar.

The age structure of the translocation population was highly skewed during T1–T3, when young palila were targeted, but it became more representative of the western population during T4–T6, when individuals were translocated regardless of age. To minimize potential disruption to the source population, we avoided moving individuals exhibiting signs of breeding or whose probable mate was not available for transport. Additionally, because we did not knowingly translocate paired birds, we could not compare the reproduction or other behavior of established pairs and newly formed pairs in the reintroduction area. Nevertheless, Armstrong *et al.* (1994) found that pair bonds or even the mutual familiarity of birds at the source site was irrelevant to the reproduction, survival, and dispersal of other translocated bird species at the release site. We were unable to predict which adults were more likely to breed, but we determined that translocated and captive-reared birds formed some productive mixed pair bonds. Although pair bonds were formed primarily among translocated birds, captive-reared males and translocated females also mated with each other. During T4–T6, 13% of the 135 translocated palila nested, and though 18% of the 28 captive-reared palila nested, no eggs of captive-reared females hatched. Four translocated females, two translocated males, and one captive-reared male produced most of the 11 fledglings observed through 2007, when monitoring was relatively comprehensive. Ten of these fledglings survived to independence, and at least one produced her own offspring, representing the F2 generation. After 2007, seven additional fledglings were observed, demonstrating the potential value of translocation as a method for reintroducing a self-sustaining population of palila.

Twenty-one translocated birds occupied the reintroduction area for at least a year, and breeding added new long-term residents to the northern population. Nevertheless, following the last translocation in 2006, the population declined and disappeared entirely by 2012, despite the annual production of offspring. We could not determine whether the attrition of birds was due more to emigration or mortality, but the northern population was declining at the same time as was the western population (Johnson *et al.* 2006, Leonard *et al.* 2008, Banko *et al.* 2009). From 2003 to 2012, spanning the entire period that reintroduced palila occupied the northern slope, the average annual rate of decline of the western palila population was 66%, or 519 birds (Camp and Banko 2012). Severe drought contributed greatly to this decline, but habitat carrying capacity was also reduced due to long-term browsing by introduced sheep (Banko *et al.* 2013). Therefore, it was not surprising that the tiny northern population disappeared five years after the last translocation and two years after the last release of captive-reared birds.

Reestablishing a Palila Population

Our translocations, supplemented by releases of captive-reared birds, founded a small breeding colony in former range on the northern slope of Mauna Kea, where palila were last reported over 40 years earlier (Walker 1968). In 1993, palila were translocated to the eastern slope of Mauna Kea to supplement the existing population at Kanakaleonui and to explore the feasibility and short-term benefits of translocation (Fancy *et al.* 1997). Palila translocated to Kanakaleonui were adults that were capable of breeding (i.e., ASY males; SY and ASY females), yet limited nesting was observed. Moreover, few translocated birds persisted in the long-term and, with no further supplementation or management, the Kanakaleonui population disappeared (Camp and Banko 2012).

Building upon the results of Fancy *et al.* (1997), our initial attempts focused on translocating young palila because we anticipated that philopatry might be less fully developed in young birds (Greenwood and Harvey 1982), resulting in longer persistence times in a new environment. We found, however, that young palila returned to the source area as frequently as did older birds and that targeting particular age classes resulted in lower rates of translocation as well as skewed population and social structure in the reintroduction area.

Fancy *et al.* (1997) translocated wild palila into a small, existing population as an initial step in developing restoration techniques, whereas we reintroduced palila to an area they had not occupied for decades. We translocated 188 palila to the northern slope of Mauna Kea in six episodes during a 10-year period (1997–2006) in contrast to Fancy *et al.* (1997), who moved 35 palila to the eastern slope in two episodes during early March 1993. Another major difference was that our translocated birds were captured, transported over paved and unpaved roads, and released on the same day, whereas Fancy *et al.* (1997) held birds in an aviary for one to three days (median = 25.1 hours; range = 1.3–69 hours) before transporting them by helicopter and releasing half immediately (hard release) and the remainder on the next day (soft release). Differences in procedures affected the weight loss of translocated birds. Weight lost by our translocated birds in T1 and T2 was less than palila moved in 1993 ($F_{3, 81} = 4.183$, $P = 0.008$), and T1–T2 birds lost more weight than did T4–T6 birds. Hawai'i 'amakihi (*Hemignathus virens*) and Japanese white-eye (*Zosterops japonicus*) also lost weight overnight when they were held in cages during trials simulating translocation in December 1996 (Work *et al.* 1999). On the other hand, although results are not strictly comparable due to differences in monitoring intensity, site persistence eight weeks after translocation was similar: 40% for the eastern birds of Fancy *et al.* (1997) and 34% for our northern birds.

Despite being moved twice as far (30–35 km, Fancy *et al.* 1997; 16 km, this study), at least 13 palila returned to the western slope from the eastern slope within one year of being translocated in 1993. Four were recaptured and nine more were re-sighted on the western slope (U.S. Geological Survey unpublished data). Palila seem to be relatively sedentary under ordinary circumstances (Fancy *et al.* 1993), so the frequent emigration of translocated birds suggests that palila strongly associate with their natal home range or that habitat or social conditions on the northern slope are not acceptable to many birds. Additionally, only 21 (11%) of our 188 translocated birds persisted in the reintroduction area for more than a year, which suggests that the western habitat is not saturated with palila.

More puzzling and difficult to verify than emigration was the behavior of birds moving back and forth between the release and source areas. The best evidence for commuting occurred during T5, when the largest number (75) of palila was translocated. Additionally, although not reported by Fancy *et al.* (1997), five birds translocated in 1993 apparently moved back and forth between the eastern and western slopes (Table 2.18). Although re-sight data can be problematic to interpret due to the difficulty in correctly identifying color band combinations, more detailed studies of the frequency of and factors, both environmental and social, influencing movement among distant parts of the range could inform dispersal models and meta-population management plans.

Translocated palila nested successfully in 1993 (Fancy *et al.* 1997) and during those trials when we moved more than just a few mature females and males. We observed nesting after moving as few as seven females (T4), and Fancy *et al.* (1997) reported nesting activity after translocating 12 females. Among potential breeders (ASY males; SY, ASY females), at least 13% (17/135) of the palila we translocated during T4–T6 nested, and 23% (8/35) of birds nested during the 1993 translocation. Thus, one can expect about one palila to nest for every four to eight that are translocated, depending on 1) environmental conditions in the release area, which are not well understood, and 2) demographic characteristics of the population of translocated birds, which are only somewhat better understood.

Table 2.18. Record of re-sightings of 1993 translocated palila that commuted.

Band number (release date)	Re-sight date	Slope	Re-sightings
74122488	04-Mar-1993	West	1
(03-Mar-1993)	25-Mar-1993	West	1
	26-Mar-1993	East	1
	08-Apr-1993	East	1
	21-Apr-1993	West	1
	27-Apr-1993	West	1
	28-Apr-1993	West	1
	18-May-1993	West	1
	23-Jun-1993	West	1
	12-Aug-1993	West	1
	06-Oct-1993	West	1
	07-Oct-1993	West	1
	18-Jul-1996	West	1
	24-Jan-1997	West	1
803175514	24-Mar-1993	West	1
(03-Mar-1993)	06-Apr-1993	(blank)	1
	19-Apr-1993	(blank)	1
	28-Apr-1993	West	3
	29-Apr-1993	West	1
	06-Jun-1993	West	2
	07-Jun-1993	West	1
	27-Oct-1993	East	1
803175806	05-Mar-1993	West	1
(03-Mar-1993)	31-Mar-1993	(blank)	1
	06-Apr-1993	(blank)	1
	No Date	West	1
	07-Apr-1993	East	1
	08-Apr-1993	(blank)	2
	09-Apr-1993	(blank)	1
	27-Apr-1993	West	1
	11-Jun-1997	West	1
	24-Jun-1997	West	1
	01-Jul-1997	West	1
	28-Apr-1998	West	1
803175813	05-Mar-1993	West	1
(11-Mar-1993)	17-Mar-1993	West	1
	26-Mar-1993	East	1
	08-apr-1993	West	2
	06-Jun-1993	West	2
	07-Jun-1993	West	1
807111401	16-Mar-1993	East	2
(03-Mar-1993)	24-Mar-1993	West	1
	26-Mar-1993	East	2
	31-Mar-1993	West	1
	06-Apr-1993	(blank)	1
	14-Apr-1993	(blank)	1
	28-Apr-1993	West	1

Band number (release date)	Re-sight date	Slope	Re-sightings
	06-Jun-1993	West	1
	16-Jun-1993	East	1

Considering the relatively short persistence of translocated populations on the northern and eastern (Fancy *et al*. 1997) slopes, the question arises as to whether either population actually transitioned through the establishment phase, when population dynamics were no longer affected by initial conditions (Grimm and Wissel 2004). In both cases, the evidence suggests that mortality and especially emigration were too great and the founding populations were too small to realize their intrinsic abilities to persist (Gusset *et al.* 2012) without additional releases of birds, stricter control of predators, and improved habitat conditions. Nevertheless, there are no realistic guidelines for determining the minimum number of palila needed to ensure a viable population (Flather *et al.* 2010). Moreover, the powerful impacts of browsing and drought, which are driving the overall decline of the palila (Banko *et al*. 2013), are difficult to mitigate in the short-term and may overwhelm efforts to reestablish populations unless habitat carrying capacity is increased sufficiently to absorb the very high level of environmental stochasticity evident on Mauna Kea.

Translocations of Other Hawaiian Passerine Birds

Understanding the results of palila translocations as well as the history of translocating other Hawaiian passerines can aid the development of realistic conservation plans for species whose populations have become stranded or widely separated in vulnerable or shrinking habitats. Seven Hawaiian passerine species besides palila have been translocated to meet various conservation goals. The Maui ʻalauahio (Drepanidinae; *Paroreomyza montana*), ʻīʻiwi (Drepanidinae; *Vestiaria coccinea*), and ʻōmaʻo (Turdidae; *Myadestes obscurus*) were translocated to test reintroduction techniques for more highly imperiled species. Both ʻīʻiwi and ʻōmaʻo were also translocated for the purpose of reintroducing a population into its indigenous range, as defined by the International Union for Conservation of Nature (2012) as “the known or inferred distribution generated from historical (written or verbal) records, or physical evidence of the species’ occurrence.” Additionally, the Laysan finch (Drepanidinae; *Telespiza cantans*) and Nihoa finch (*T. ultima*) were translocated to other tiny atolls and islands in the Northwestern Hawaiian Islands where they once may have occurred based on general ecological similarities (U.S. Fish and Wildlife Service 1984, Morin and Conant 2002). Recently, the Nihoa millerbird (Sylviidae; *Acrocephalus familiaris kingi*) was translocated to Laysan Island to replace the extinct Laysan millerbird (*A. f. familiaris*; Farmer *et al.* 2012). The most unusual example was translocating a single poʻo-uli (Drepanidinae; *Melamprosops phaeosoma*) in the hopes of bringing together two of the last three dispersed individuals (Groombridge *et al.* 2004a).

The Laysan and Nihoa finches are closely related to palila, but they are generalist seed-eaters rather than specialists and inhabit coastal shrub-grassland rather than forest. Despite marked differences in the habitats they have occupied historically, palila and Laysan finch once shared the same coastal habitat at Barbers Point, Oʻahu (Olson and James 1982). The Nihoa finch and other finch-billed Hawaiian honeycreeper species also occupied coastal habitats in the main Hawaiian Islands prehistorically (James and Olson 1991, Burney *et al.* 2001). The generalist habits of both Laysan and Nihoa finches would seem to make them suitable candidates for reintroduction into the main Hawaiian Islands (Morin and Conant 2002); however, reintroducing the specialist palila to lowland sites would require the creation of suitable habitat, undoubtedly at great expense of time and resources. Furthermore, birds reintroduced to lowland sites would require protection from mosquito-borne diseases and mammalian predators that were not present prehistorically. Whether or not Laysan and Nihoa finches are returned to the main islands, their translocation to other tiny islands indicates hardiness during transport aboard ships and adaptability in new environments. The translocation in 1967 of 108 Laysan finch 460 km to Pearl and Hermes Reef established a small population that has persisted for more than 40 years (Berger 1981, Conant 1988, Morin and Conant 2002, U.S. Fish and Wildlife Service 2008). Unspecified numbers of Laysan finch translocated to Midway Atoll in 1891 apparently did not persist long, but birds translocated there in about 1905 established a population that persisted until about 1944, when they were extirpated by rats that were inadvertently introduced during WWII (Fisher and Baldwin 1946, Bailey 1956). The translocation in 1967 of 42 Nihoa finch 450 km to Tern Island (32 birds) and East Island (10 birds) in French Frigate Shoals failed to establish long-term populations. Birds on East Island were never seen again, and though some pairs nested on Tern Island in 1968, the population eventually disappeared (Berger 1981, U.S. Fish and Wildlife Service 1984).

The millerbird, subspecies of which are endemic to Nihoa and Laysan in the Northwestern Hawaiian Islands, is the only representative of the Old World warblers in the Hawaiian Archipelago (Morin *et al.* 1997). Named for the "miller moths" it readily catches, the millerbird is a generalist insectivore that gleans native and non-native insects from shrubs and other plants. The Laysan millerbird was extirpated in the 1920s after ecosystem destruction by introduced rabbits and livestock. The population of Nihoa millerbirds on Nihoa was estimated at 400 individuals in 2012 and has historically fluctuated between 30–800 birds. The American Bird Conservancy, U.S. Fish and Wildlife Service, and other partners translocated 24 adult millerbirds from Nihoa to Laysan Island in 2011 and another 26 adults in 2012. The translocations were the culmination of over five years of research and more than 20 years of habitat restoration on Laysan. Millerbirds were captured over 1.5 days on Nihoa and were transported three days by sea to Laysan, over 1,000 km from Nihoa, in a modified vessel cabin. Birds were held in captivity from 4.5–6 days. All 50 birds survived the translocation and their survival on Laysan has been high. The 2011 cohort bred throughout 2012, producing at least 29 juveniles that overwintered with little mortality. At least 50 fledglings were produced through 2013, bringing the total population on Laysan to over 120. These preliminary results suggest that the two translocations have resulted in the reestablishment of millerbirds on Laysan.

Maui ʽalauahio were transported by foot over rough terrain to near (1 km; *n* = 8 birds) and distant (2.5 km; *n* = 10 birds) release sites in montane rain forest to evaluate stress and help inform managers of the potential risks of translocating the critically endangered poʽo-uli (Groombridge *et al.* 2004a). Not surprisingly, most (11/16) translocated Maui ʽalauahio returned to the capture site within five days, and the remainder returned within several weeks. The Maui ʽalauahio study involved relatively short distances to simulate conditions anticipated for moving one of the last two known female poʽo-uli from her home range about 1.5 km into the territory of the last known male (Groombridge *et al.* 2004b). In that attempt, the female was released into the male's home range at dusk, but on the following day she returned to her home range without any indication that the two birds had detected one another.

ʽĪiwi were translocated by helicopter from East Maui to West Maui in 2001 to evaluate techniques that might be used to recover the endangered ʽakohekohe (Drepanidinae; *Palmeria* *dolei*) and to reestablish an ʻiʻiwi population in its former range (Becker *et al.* 2010). Eighteen ʻiʻiwi were transported about 50 km from their home ranges with nine being released immediately ("hard" release) and nine being held in field aviaries for a week before being released ("soft" release). The nine ʻiʻiwi that were released one hour after transport established themselves near the release site and survived the entire monitoring period (21 days, based on average transmitter lifespan). Three of the nine soft release ʻiʻiwi died in captivity before release, possibly due to exposure during stormy weather. The surviving soft release birds tended to move farther away from the release site, generally avoiding areas occupied by hard release birds, which were already established in the reintroduction area, suggesting interference competition. Although it seems unlikely that a population was reestablished as a result of the translocation, it also seems unlikely that any birds returned to East Maui. ʻĪʻiwi sometimes move substantial distances across the landscape in search of nectar (Perkins 1903, Baldwin 1953, MacMillen and Carpenter 1980, Ralph and Fancy 1995, Berlin *et al.* 2001, Hess *et al.* 2001), but a great expanse of unsuitable habitat for native forest birds separated the source and reintroduction sites.

Wild, adult ʻōmaʻo were translocated, and captive-reared ʻōmaʻo were released in former range on Hawaiʻi Island in 1996 to compare reintroduction techniques that might be applied to the endangered puaiohi (Turdidae; *Myadestes palmeri*; Fancy *et al.* 2001). Sixteen ʻōmaʻo were driven over roads from several windward sites to a drier, leeward site and released on the day of capture ("hard" release) or after one to nine days of holding ("soft" release). Four birds died within 48 hours from handling or transport stress, but no other mortalities were observed during 30 days of monitoring. Most (8/12) birds dispersed 2–5 km in the first three days, but three birds eventually returned to the release site. Three of four translocated birds held in a hacking box for seven to nine days did not disperse after being released, and the one that did disperse returned to the release site after a week. Twenty-five captive-reared, young (57–66 days of age) ʻōmaʻo were released in the same area after six to nine days of acclimatization. Although four were killed by predators after release, the remainder survived the 30-day monitoring period. Captive-reared ʻōmaʻo were more faithful to the reintroduction area. Reproduction was observed within the first year, but few birds could be detected two years after the reintroduction, and a population was not reestablished.

Trials involving these seven species demonstrate a wide range of responses by Hawaiian passerine species to different aspects of confinement, transport, release, and life in new areas. Nevertheless, some general conclusions can be drawn. For example, some generalist species (*sensu* Banko and Banko 2009), notably the Laysan finch and Nihoa millerbird, seem ideal candidates for reintroduction due to their apparent hardiness during transport and their ability to opportunistically forage and quickly adapt to different environments after release. On the other hand, establishing populations of species that are more specialized in terms of diet and habitat use, such as the palila and the ʻiʻiwi, may require repeated releases of individuals and intensive habitat management to increase carrying capacity and reduce predation. The same approach also may be needed to reestablish populations of ʻōmaʻo, which, despite having a relatively generalist diet, are highly sedentary and perhaps sensitive to microhabitat conditions. The distance between capture and release sites undoubtedly influences the persistence of birds in the reintroduction area and the frequency at which they return to the source area. Even so, moving birds relatively short distances may result in movements that ultimately serve to connect subpopulations, as illustrated by our translocation of palila. Of the three release trials comparing soft and hard releases, only for ʻōmaʻo (Fancy *et al.* 2001) were the results of soft release superior, but only one day of holding was involved in the soft release of palila in 1993

(Fancy *et al.* 1997). Although not the case with the more generalized species, prolonged confinement of specialized species in cages or field aviaries before or after transport may increase their risk of dying or becoming debilitated (Fancy *et al.* 1997, Becker *et al.* 2010).

Although the success of reestablishing populations of birds should depend largely on the effectiveness of reducing threats and improving habitat conditions, Hawaiian forest bird management is typically limited in its spatial and temporal scope and in the range of threats that are addressed (Banko *et al.* 2001, Pratt *et al.* 2009, Price *et al.* 2009). In the case of palila, predator control was an integral aspect of the reintroduction effort. Nevertheless, some translocated birds were killed or scavenged, and the consequences of losing even a few birds from the pool of potential long-term residents or suitable mates, for example, are unknown. A more far-reaching issue is protecting habitat from browsing ungulates. Several centuries of browsing by cattle (*Bos taurus*), sheep (*Ovis aries*, *O. gmelini musimon*, and hybrids), goats (*Capra hircus*), and disturbance by pigs (*Sus scrofa*) lie at the heart of the palila conservation dilemma (Banko *et al.* 2009). Habitat destruction presumably was the main factor leading to the extirpation of palila outside the western slope, and sheep continue to degrade palila habitat (Banko *et al*. 2013). Nevertheless, thinning of the sheep population has allowed māmane to regenerate, which made palila reintroduction on the northern slope seem worthwhile, if only as a pilot project. The persistence of a small breeding colony of palila five years after the last translocation trial suggests that focused, sustained habitat management could lead to a viable population again on northern Mauna Kea. A program to restore habitat on the northern slope is underway (Banko *et al.* 2009), and the removal of sheep from palila habitat should allow natural regeneration to connect the western and northern slopes in future decades. The dire consequences of drought for palila (Banko *et al.* 2013) warrant accelerating and expanding restoration activities.

Conclusions and Implications for Future Translocations

Our results demonstrated that translocation has promise as a means for reestablishing palila in former range, provided that habitat carrying capacity can be increased. The small breeding colony that was founded might have persisted much longer with additional periodic infusions of birds. Nevertheless, substantially slowing the rate of attrition at a time when the source population itself was declining rapidly (Banko *et al.* 2013) would seem to be an unrealistic goal. Many birds were lost to emigration probably because of the proximity of the source area to the reintroduction area and because of the greater availability of habitat on the western slope. Translocating birds to more distant sites (i.e., off Mauna Kea) or better quality habitat might increase persistence and reduce emigration, although the movement of some birds between sites that we observed may be desirable to facilitate gene flow between subpopulations. At least one individual that was not translocated also moved among the source and reintroduction areas, suggesting that some palila occasionally explore distant areas or possibly that their long-distance movements are influenced in some way by translocated birds. Sex, age, and cohort size did not predict how long or whether individuals were likely to remain in the reintroduction area. Translocating a cross-section of the source population will create a relatively normal social environment compared, for example, to even-aged cohorts, and translocating mature individuals, with attention to maintaining approximate parity in the sex ratio, will likely lead more quickly to breeding in the reintroduced population.

We found no correlation between persistence and the numbers of birds translocated, but we did not move more than 75 birds in a trial, and birds were moved individually or in small groups (2–13) over several months, resulting in relatively low palila densities even in habitat patches where they tended to concentrate. Fancy *et al.* (1997) obtained similar results by translocating 35 palila in two cohorts within eight days of each other. Reintroduction success has been associated with large numbers (>100) of translocated animals (Wolf *et al.* 1998, Fischer and Lindenmayer 2000), but there are practical constraints to moving large numbers of palila and most other endangered species. Nevertheless, increasing the numbers of birds captured and translocated per unit of time would allow birds to accumulate more quickly in the release area, possibly with some increase in persistence and breeding. Even so, if birds are to be held in field aviaries before or after transporting them, protocols are needed to reduce stress. Fancy *et al.* (1997) held palila up to 69 hours in field aviaries in order to translocate sizeable groups, but weight loss resulted in the deaths of some birds. There also could be limits on the number of birds translocated due to density-dependent constraints in the reintroduction area, especially if the habitat is still recovering from environmental disturbance (Armstrong and Ewen 2002).

Relatively few translocated palila bred, but those that did had productive nests, and some nested frequently breeding pairs nested frequently and productivity. Reproduction may be elevated in colonizing populations due to density-dependent factors such as food competition being initially weak (Brouwer *et al*. 2009). Although habitat on the northern slope of Mauna Kea was much more limited and fragmented compared to habitat on the western slope, edaphic conditions in the deep, fine ash (Wolfe and Morris 1996) might have reduced the impact of drought on māmane seed production (Banko *et al*. 2013). Nevertheless, breeding activity in the translocated birds also may have been stimulated by the change in their social environment. The small cohorts of captive-reared birds that were released contributed marginally to the growth and persistence of the reintroduced colony, although two males added notably to the number of fledglings produced. Assuming that captive-reared females also can breed successfully, releasing larger numbers of birds may be the key to improving the effectiveness of captive propagation in restoring wild populations.

The translocation trials were informative about habitat conditions on the northern slope. The limited amount of high-quality habitat undoubtedly reduced the size and persistence of the reintroduced colony, yet the production of a small F2 generation demonstrated the potential for supporting a viable population in the near future, assuming that habitat restoration continues. The long-term persistence of palila on the northern slope depends largely on the year-round availability of māmane seeds and other foods. Introduced ungulates continue to degrade the area despite some recruitment of māmane and other native trees and shrubs (see Chapter 25: Vegetation Survey in Palila Critical Habitat). Planting trees and controlling weeds to increase māmane density and widen the band of forest around Mauna Kea would speed habitat recovery and increase the availability of food (Banko *et al.* 2002a). Management to prevent or reduce impacts from fire (Thaxton and Jacobi 2009), forest disease (Gardner and Trujillo 2001), and introduced food competitors such as ants (see Chapter 22: Threats to Food Resources: Ants), parasitoid wasps (Brenner *et al.* 2002, Oboyski *et al.* 2004; see Chapter 19: Threats to Food Resources: *Cydia* Caterpillar Parasitism), and predacious wasps (see Chapter 21: Threats to Food Resources: Yellowjackets) may also benefit population restoration. The recent decline of the palila population on the western slope underscores the urgency of increasing habitat carrying capacity (Banko *et al.* 2013).

Although we removed predators in the reintroduction area, some birds were nonetheless killed, which affected our results during T2 particularly, when radio transmitter entanglement may have contributed to the problem. Predation by feral cats (*Felis catus*) may account for the annual loss of about 11% of palila nestlings and an unknown number of adults (Banko *et al.*

2002b, Banko *et al.* 2009), but the loss of birds has disproportionately large demographic consequences for small colonies of birds. Reducing mortality factors is important to the success of re-introductions (Wolf *et al.* 1998, Fischer and Lindenmayer 2000), and more effort is needed to protect palila (Banko *et al.* 2009).

Translocation likely had little impact on the source population because many birds emigrated back to the western slope and relatively few birds died. Protecting the core palila population on the western slope will likely continue to be the main goal for palila conservation for the foreseeable future. Nevertheless, reclaiming lost range on Mauna Kea and elsewhere before the single and highly vulnerable population dwindles to the point where recovery options become greatly reduced could significantly advance palila conservation.

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3 HARVESTING WILD EGGS AND SUPPLEMENTING FOOD AT NESTS

Paul C. Banko, Luanne Johnson, Steve J. Dougill

Introduction

The palila (*Loxioides bailleui*) could benefit from population management because its low reproductive rate constrains population growth. Additionally, its association with relatively large trees and high canopy cover (Scott *et al.* 1984) suggests that even as habitat conditions improve, the palila's recovery will be slow without active population management (Banko *et al*. 2009). Moreover, until habitats have been restored at the landscape scale, intermittent population management may be required to sustain small enclaves of palila in habitat fragments and reintroduction sites, such as on the northern slope of Mauna Kea or at Kīpuka ʻAlalā.

Various techniques may be suitable for maintaining and bolstering small populations of palila, including captive-rearing and release of birds from wild-harvested eggs (rear-and-release). Rear-and-release was one of the methods used during the 1990s to forestall the extirpation of ʻalalā (*Corvus hawaiiensis*) in South Kona (Banko 2009). Although the wild population eventually died out, rear-and-release was shown to be a promising management option that might aid the recovery of other species (Lieberman and Kuehler 2009).

In collaboration with the San Diego Zoo Institute for Conservation Research (SDZICR) and the U.S. Fish and Wildlife Service (USFWS), we explored the feasibility of rear-and-release as a tool in recovering palila by harvesting wild eggs and rearing the chicks in captivity. Although none of the resulting juveniles or young adults was released to the wild, the small colony became the nucleus of a captive-breeding program that generated palila for release (Lieberman and Kuehler 2009; see Chapter 4: Release and Monitoring of Captive-Reared Palila). Years later, three of the wild-egg captives were released to the wild.

To investigate another potential technique for enhancing palila populations, we supplemented the diets of wild nestlings to assess changes in growth and survival rates. Palila chicks spend 21–30 days in the nest (Pletschet and Kelly 1990, Banko *et al*. 2002a) and are thus exceptionally vulnerable to predators and storms. We hypothesized that a diet consisting mainly of seeds and a low level of protein from insect prey might contribute to slow nestling growth. We attempted to provide extra insects to supplement the diet and increase the growth and survival of nestling palila in 1996, but we terminated the effort after concluding that it was not feasible to climb trees to regularly provision wild nestlings. During the 1998 nesting season, we experimented with ways to offer supplemental food to nesting adults, anticipating that they would in turn feed their offspring. In addition, we observed natural rates of provisioning at nests to gain insights for developing supplemental feeding techniques.

Methods

Wild Egg Harvest

Nests were located while searching along or off transects in 1996 and 2000 (see Chapter 9: Breeding Phenology, Productivity, and Nesting Success). When we knew the date that eggs were laid, we timed clutch removal for the second half of the incubation period in order to maximize the amount of natural incubation and probability of hatching success. Standard 12 m, five-shelf, mist-nets were set around the nest tree prior to clutch removal, but nets were not opened until after the clutch was removed. We observed nests from a blind or from a distance (>10 m) until the female flew off the nest during a natural recess. We then approached the tree, climbed to the nest, removed the clutch, and replaced it with wooden eggs that were approximately the same size, shape, and color as palila eggs. The wild eggs were removed from the nest by hand and embedded, blunt end oriented upward, in sterilized millet seed that was kept warm inside an insulated container. The container with the eggs was lowered to SDZICR staff on the ground, who transported it to the Keauhou Bird Conservation Center (KBCC). Mist-nets were opened after the wooden eggs were in place and there was no longer any risk to the natural clutch.

All females were captured between 17 April and 28 June 1996 and were uniquely marked with three color-bands and one USFWS aluminum band. Before removing the wooden eggs and releasing the female, we attached 1.5–1.8 g radio transmitters with a chiffon patch and surgical skin adhesive (Fancy *et al.* 1993).

Females were tracked and observed within the first 24 hours of release to ensure they were alive and had no difficulties with their transmitters. They were then observed every 1–5 days for evidence of re-nesting. They were not followed for longer than 20 minutes at a time to prevent disturbing any re-nest attempt. The first day of egg laying in subsequent nests was calculated by subtracting 16 days, the average incubation interval (van Riper 1980), from the hatch date. The fates of all re-nests that could be monitored were evaluated by visiting the nest every 3–5 days. Eggs that did not hatch were collected and opened to assess fertility. All nests were mapped to 10.0 m with a GPS (global positioning system) unit, and distance to re-nests was measured using GIS (geographic information system).

The incubation of eggs and rearing of chicks in captivity were carried out at the KBCC (Lieberman and Kuehler 2009).

Supplemental Feeding

To determine the effect of extra insect food on chick growth and survival, we selected nests in 1996 containing two chicks that we could access relatively easily. We observed the nest from a concealed location at least 20 m away to determine when the female departed on recess and never intentionally flushed the female from the nest. While the female was absent, we climbed to the nest and removed the chicks to measure tarsus, culmen, and body weight and to score body fat and stage of development. We banded chicks after age 10 days, or if younger, made a mark with non-toxic ink on the underside of the lightest chick, designated the "B" chick. We fed the B chick cricket abdomens (provided by KBCC) whenever opportunities permitted and recorded changes in growth parameters on days when feedings were provided. There were no opportunities to supplement the diet of nestlings in 1997 because natural chick mortality was high. We did not attempt supplemental feeding at nests after 1999.

Fresh māmane (*Sophora chrysophylla*) pods, flowers, and seeds were made available to adults at nests in 1998 to determine whether they would feed their chicks with the food provided. A telescoping pole fitted with a natural perch and a shallow cup containing the food items was gradually moved to ≤1 m of the nest when both adults were absent from the area. Staff observed adult behavior at the nest from a blind placed 15 m from the nest tree and replaced food twice each day.

Results

Wild Egg Harvest

We collected a total of 32 eggs from 17 wild nests in 1996 for captive propagation. Of these 32 eggs, 20 eggs were removed from 10 nests where we replaced the clutch with wooden eggs, radio-tagged the female, and monitored her subsequent nesting behavior. The time that females (*n* = 10) incubated wooden eggs before transmitter attachment ranged from 2 hours to 6 days. Of the ten transmitters attached to females, two failed soon after release and two detached before a new nest could be found. The six remaining females re-nested with incubation of new clutches beginning 19.83 ± 2.71 SD days after transmitter attachment (range = 16–23 days). Original nests were never reused, and subsequent nests were located 239.17 ± 238.25 SD meters from previous nests (range = 112–720 m). Mean clutch size of re-nesting females declined from 2.0 to 1.7 ± 0.52 SD.

Of the 20 eggs removed from the nests of monitored females, five were either infertile or contained dead embryos (C. Kuehler and A. Lieberman, SDZICR, personal communication). Ten eggs were laid in the six re-nests. Two of these six nests yielded a total of three fledglings, two nests were harvested for captive propagation at KBCC (three eggs resulting in two chicks), one nest with two eggs failed due to embryo mortality, and one nest was depredated before the viability of the single egg could be determined.

We originally anticipated that the 1996 chicks would be released on the northern slope of Mauna Kea after they had developed adequate feeding skills. Instead, these birds were kept as breeding stock because only 11 of the original 21 chicks fledged. The other chicks died, apparently from infection by bacteria or other pathogens (see Chapter 7: Disease). We collected an additional four eggs from two wild nests in 2000. Although all eggs were fertile, one contained a dead embryo. Three chicks hatched and all fledged, and all were maintained in captivity at KBCC (C. Kuehler and A. Lieberman, SDZICR, personal communication).

Important milestones in developing captive propagation techniques for palila were met at KBCC in 2000 when the birds reared from wild-harvested eggs produced fertile eggs, chicks, and fledglings. During 1996–2007, 135 eggs were laid in captivity (99) or were harvested from the wild (36) and 96 contained live embryos (Lieberman and Kuehler 2009). From these viable eggs, 76 chicks hatched (79%) and 54 (71%) survived to independence.

Supplemental Feeding

We provided cricket abdomens to the smallest chick in five nests. Although at least one chick fledged from all treated nests, results were not meaningful due to the small sample size and the limited rate at which we could provision nestlings. We provided a maximum of ten feedings over seven days per nest, and only one feeding was provided at two nests. Two supplemented chicks disappeared from their nests. The chick that disappeared ten days after hatching possibly had a bacterial infection (i.e., yolk sac infection) because it grew very slowly, had a weak feeding response, and strained to defecate during its final week of life. The other chick disappeared within four days of its only feeding of two cricket abdomens. In 1998, māmane flowers, pods, and seeds that we made available to adults at two nests were ignored.

Discussion

Wild Egg Harvest

Harvesting eggs from wild palila nests resulted in re-nesting within about three weeks in locations near the original nest site with little net loss in the productivity of the affected wild pairs. Because palila nests are readily apparent from the ground and can be frequently accessed by climbing, rear-and-release techniques might be developed into a feasible method of bolstering populations. For example, eggs could be harvested from many nests relatively quickly in years of abundant food, and the resulting birds could be released when wild fledglings are gaining independence from their parents. Given the frequency of re-nesting by manipulated pairs and assuming at least moderate survival of the captive-reared birds, the net gain in young birds could be substantial. The captive propagation program that developed from the harvest of wild eggs resulted in the release of only 28 palila during 2003–2009 (see Chapter 4: Release and Monitoring of Captive-Reared Palila), suggesting that wild egg harvest for captive-reared release might be a more effective option for boosting population numbers.

Supplemental Feeding

Supplementing the diets of palila chicks was logistically difficult, and we were unable to evaluate the effects of extra insect food on chick growth and survival. The technique was difficult to apply at wild nests because opportunities to feed chicks was limited by the number of female recesses, accessibility of the nest, and availability of people who could safely climb trees and handle chicks. We also decreased the pool of eligible nests by removing clutches from 17 nests for captive propagation in 1996.

Supplemental food (māmane seeds and *Cydia* caterpillars) offered in close proximity to nests in 1998 was ignored by adult palila. Although we have hand-fed both food types to palila captured in mist-nets, nesting adults may ignore supplemental food in close proximity to their nest because our observations indicate that they rarely forage in the nest tree. Ignoring food close to the nest may be a strategy to minimize activity in the nest tree to avoid attracting aerial nest predators, such as ʻio (*Buteo solitarius*) and pueo (*Asio flammeus*). Additionally, māmane seeds contain high levels of potentially toxic alkaloids (Banko *et al.* 2002b), and palila may be highly selective about the seeds they feed to their young.

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4 RELEASE AND MONITORING OF CAPTIVE-REARED PALILA

Chris Farmer, Paul C. Banko

Introduction

Palila (*Loxioides bailleui*) are in danger of extinction because they are declining in numbers and are concentrated on the western slope of Mauna Kea (Jacobi *et al.* 1996, Banko *et al.* 1998, Gray *et al*. 1999, Johnson *et al.* 2006, Leonard *et al.* 2008, Banko *et al.* 2009, Banko *et al.* 2013, see Chapter 5: Population Trends and Response to Environmental Factors). Small populations are at a greater risk of extinction due to increased vulnerability to avian disease, habitat degradation, and natural disasters such as fire, severe storms, or drought. Models of the dynamics of small populations have demonstrated demographic accidents and environmental disturbances as two major causes of extinction (Leigh 1975, Goodman 1987). To recover the species, the Hawaiʻi Forest Bird Recovery Plan recommends that palila exist in at least three populations (U.S. Fish and Wildlife Service 2006). At the request of the U.S. Fish and Wildlife Service (USFWS), we evaluated translocation as a technique for reintroducing palila to former range on the northern slope of Mauna Kea (see Chapter 2: Translocating Wild Palila). Also at the request of USFWS, we assisted with monitoring the survival and behavior of captive-reared palila that were released near Puʻu Mali on northern Mauna Kea by the San Diego Zoo Institute for Conservation Research (SDZICR).

The Keauhou Bird Conservation Center (KBCC) was established in 1993 with the goal of propagating and reintroducing threatened species of Hawaiian birds to their native ranges (Lieberman and Kuehler 2009). Originally operated by The Peregrine Fund, KBCC is now operated by SDZICR. The SDZICR released a total of 28 captive-reared palila: ten in December 2003, five in December 2004, six in November 2005, and seven in March 2009. Captive-reared palila were monitored to determine survival, home range, behavior, and any nesting effort. Four or five months following the releases of captive-reared palila, we translocated 32 birds in 2004, 75 in 2005, and 28 in 2006 from the western slope of Mauna Kea (see Chapter 2: Translocating Wild Palila).

In this report, we provide a more detailed account of the results of the 2003 and 2004 releases, which were monitored closely. We also summarize some of the data collected from the 2005 and 2009 releases.

Methods

Preparation

In 1996, to stock KBCC with palila for captive propagation, we collected 32 eggs from 17 wild clutches on the western slope of Mauna Kea (see Chapter 9: Breeding Phenology, Productivity, and Nesting Success; and Chapter 3: Harvesting Wild Eggs and Supplementing Food at Nests). During 30 July–17 August 2007, we assisted the SDZICR, USFWS, and Hawaiʻi Division of Forestry and Wildlife by capturing five wild, adult palila (three females, two males), which were added to the captive flock at KBCC. The SDZICR developed techniques for incubation and captive rearing of palila (Lieberman and Kuehler 2009).

Prior to transport from KBCC to the release site, a veterinarian performed a standard avian physical. He examined blood and fecal samples to determine fitness for release and to protect the wild population from infection or disease.

Our research suggested to USFWS that the northern slope of Mauna Kea was suitable for reintroduction based mainly on the trade-offs of liabilities and assets, including the quality of habitat and food available to released birds, the potential for habitat restoration along a substantial gradient of elevation, and the lower threat of human disturbance and fire (Beck 1992; see Chapter 1: Evaluating Sites for Reintroduction).

Release

The SDZICR constructed two hack towers (Hack Tower 1 and Hack Tower 2), which are elevated predator-proof aviaries (Tweed *et al.* 2002). The hack towers were separated by 250 m and located near Hawaiʻi Forest Bird Survey Transect 116 on the northern slope of Mauna Kea. Helicopters were used by SDZICR to transport the palila to the release site. The birds were soft-released, meaning each cohort spent three weeks inside a hack tower to acclimatize to local environmental conditions, become familiar with landmarks, recuperate from transportation, and establish social and reproductive bonds (Beck 1992). The SDZICR routinely monitored the birds while in the hack towers to determine their overall well-being and acclimatization to the new environment.

Ten palila were released in two cohorts (Cohort One and Cohort Two) in December 2003. Single cohorts were released in December 2004 (five birds), November 2005 (six birds), and March 2009 (seven birds).

The SDZICR provided supplemental food to the birds post-release to facilitate the transition to feeding and sheltering in the wild (Lieberman and Kuehler 2009). The prepared food pans contained scrambled eggs, baby food, apples, oranges, and papaya. Initially, the SDZICR provided supplemental food two times a day, gradually decreasing to once a day, and then to one time per week. For the 2003 release, we assisted with the distribution of food at each hack tower and monitored the towers to determine if any of the released captive birds consumed the food. We concluded the monitoring of supplemental feeding in the beginning of February 2004. The SDZICR staff was solely responsible for the food distribution in 2004, 2005, and 2009.

Monitoring

Prior to release, the SDZICR marked each bird with a unique combination of three color bands and one numbered aluminum band to facilitate monitoring. They also fitted each bird with a lightweight radio-transmitter (model BD-2, Holohil System Ltd.) weighing <5% of its body weight. The SDZICR attached transmitters using an elastic figure-8 harness (Rappole and Tipton 1991).

With our assistance, SDZICR staff monitored birds for about 30 days following their release, and we continued frequent monitoring until 2007, then quarterly monitoring until 2009, and irregular monitoring until 2012. We collected location data by radio-tracking and re-sighting with binoculars. We collected behavioral observations and identified roost sites for both 2003 cohorts. We plotted the distance of the birds from the hack tower on a daily basis when feasible. If we located a bird more than once per day, we randomly chose one of the locations to represent that day. We collected māmane (*Sophora chrysophylla*) pods to examine the captive birds' foraging behavior. We observed the birds for a minimum of eight to ten weeks (standard battery life of transmitters) after release and recaptured some birds to replace their transmitter to allow additional monitoring. We recorded behavioral interactions between captive-reared and wild-caught translocated palila.

Results

We searched for captive-reared birds after their release on the northern slope of Mauna Kea with declining effort through 2012 and observed the last individual in December 2010. Although we recorded locations of captive-reared birds whenever they were observed, here we focus primarily on the results of the survival and behavior of birds released in 2003 and 2004 through September 2005.

Before the 2003 release, a veterinarian found nematode ova (*Capillaria* sp.) in the fecal samples of six captive birds. He reviewed the results and recommended the release of the birds (S. Grune, DVM, Big Island Pet Care, personal communication via T. Goltz, SDZICR). Two birds were found dead two days after they were released, with no evidence of depredation. We assume that two other individuals from the 2003 release died because we did not detect female C3.26 after 12 December 2003 or female C3.07 after 16 March 2004 (Table 4.1). Another bird's transmitter failed to function four days post-release, but we determined that it was alive. We tracked seven birds, including C3.26, for an average of 18 weeks post-release. We recaptured five birds in the last week of February 2004 and affixed new transmitters to extend the monitoring period. Additionally, one bird received a new transmitter in the second week of May 2004, and a second replacement transmitter in August 2004.

Table 4.1. Detection patterns of captive-reared birds on the northern slope of Mauna Kea with total and maximum days observed and mean time between observations. Observations were derived from radio-tracking and re-sight data between 8 December 2003 and 30 September 2005.

Bird ID number	Hatch year	Sex	First observation	Last observation	Total days obs.[†]	Max days between obs.[†]	Mean time (days) between obs.
C3.03	1996	M	16-Dec-03	10-May-05	37	123	18
C3.07	1996	F	15-Dec-03	16-Mar-04	42	27	2
C3.25	1996	F	20-Dec-03	3-Jul-05	40	289	14
C3.26	2000	F	8-Dec-03	12-Dec-03	5	1	1
C3.36	2000	M	8-Dec-03	4-Jul-05	63	95	9
C3.38	2001	M	9-Dec-03	21-Sep-05	78	143	8
C3.42	2001	F	9-Dec-03	2-Aug-05	51	245	12
C3.44	2002	M	15-Dec-03	8-Sep-05	60	149	11
C4.45	2003	F	16-Feb-05	16-Feb-05	1	0	0
C4.48	2004	F	28-Mar-05	29-Sep-05	22	105	9

[†] Includes only one observation per day

Of the five palila in the 2004 release cohort, three died within 3–6 days of release. The remains of two birds were heavily scavenged. The transmitter of one bird was cracked, suggesting cat depredation (P. Buchholz, SDZICR, personal communication). The SDZICR found the third carcass to be in fair condition with little scavenging and no evidence of depredation. We recaptured female C4.48, affixed a new transmitter to her, and tracked her until 27 April 2006 (not shown in Table 4.1). We recovered no carcasses of birds released in 2005 or 2009; thus, we could not determine timing or causes of mortality.

We re-sighted some birds long after their radio transmitters had expired, although our monitoring effort declined markedly after 2007 and again after 2009. The longest-lived bird was male C3.44 (one color band was missing but C3.44 was the most likely candidate due to its long history of re-sightings on the northern slope). C3.44 was last observed on 8 Dec 2010, seven years after his release. The last bird observed from the 2004 release was female C4.48, who was seen on 31 May 2006, 1.5 years after her release. Of the 2005 release group, male C5.59 was last seen on 9 September 2010, 4.8 years after being released. Birds released in 2009 disappeared quickly; the last bird observed was female C9.94 on 29 July 2009, just over four months after her release.

Movement

The 2003 release birds demonstrated strong site fidelity to the hack tower area during the initial eight-week radio-tracking period. We monitored the distance that Cohort One birds had moved away from Hack Tower 1. For three weeks post-release, most birds stayed within 1,100 m of the hack site. After four weeks, one bird spent nearly a week 4,500 m distant from the hack site. One female exhibited territorial behavior centered on Hack Tower 1 by chasing a male out of the tower and away from the food pans. The birds decreased their visits to the hack sites as supplemental food was provided less frequently. We did not observe the birds at the food pans four weeks post-release.

During the first two weeks post-release, we did not observe any birds from Cohort Two farther than 1,019 m from Hack Tower 2. One female did not go beyond 1,019 m of Hack Tower 2 for 13 weeks post-release, and one male was not observed farther than 857 m away for 20 weeks post-release. We observed the other male farther than 2,000 m from Hack Tower 2 for 16 days; he traveled as far away as 2,277 m.

The 2003 release birds continued to display site fidelity to the hack towers in the fall of 2004 and the spring and summer of 2005. Based upon re-sight data, most individuals remained within 400 m of their respective hack towers. The mean distance from the hack tower for C3.38 (677 m) was greater than the mean distance for all other 2003 birds (262 m), and this male traveled as far as 1,090 m away. C3.25 moved between 110 m and 733 m from his hack tower, which was consistent with the initial tracking data for this bird after his release in 2003. One male (C3.44) and one female (C3.42) moved mean distances of 180 m and 189 m, respectively, and the final two males (C3.36 and C3.03) stayed closest to the towers with mean distances of 94 m and 130 m.

For the 2004 cohort, we re-sighted C4.48 at a mean distance of 820 m (n = 6 observations) from the hack site. We did not obtain location information for the remaining bird from the 2004 release.

Vegetation Use

During 2003–2005, captive-reared palila (n = 11) were detected in māmane trees 90.7% of the time on average (Table 4.2). Birds were observed in koa (*Acacia koa*) 5.0% of the time. Most (92%) koa observations were of two individuals (C3.07 and C3.44), who were detected in koa on 31% and 13% of the occasions, respectively. Naio (*Myoporum sandwicense*) utilization was lowest at 1.4% and other plant species were recorded only 1.8% of the time.

Foraging Behavior

During the early 2004 tracking observations, we noticed that the method of extracting seeds from māmane pods varied among the seven captive-reared palila that were released in 2003.

Table 4.2. Use of tree species by captive-reared palila by sex and age. Data shown are total number of observations, number of detections in each species of tree, and percentage of detections in māmane. Observations were derived from re-sighting and tracking data through 30 September 2005.

Bird ID number	Hatch year	Sex	Total obs.[†]	Māmane	Naio	Koa	Other species	Percent in māmane[‡]
C3.03	1996	M	51	48	0	0	0	100
C3.07	1996	F	57	28	0	13	1	67
C3.25	1996	F	57	51	0	1	0	98
C3.26	2000	F	10	10	0	0	0	100
C3.36	2000	M	95	83	1	1	0	98
C3.38	2001	M	97	91	2	0	2	96
C3.39	2001	F	5	4	0	0	1	80
C3.42	2001	F	79	74	0	0	1	99
C3.44	2002	M	79	62	0	10	3	83
C4.45	2003	F	2	2	0	0	0	100
C4.48	2004	F	23	18	4	0	1	78

[†] Includes observations without specified vegetation

[‡] Percent in māmane is calculated from observations with vegetation data, not total observations.

Examining pods after they had been opened by the captive-reared bird revealed that only one bird was extracting seeds in the manner of wild palila while the other six were extracting seeds differently. The unusual method of seed extraction involved the bird pecking at the pod to expose and eat each seed, whereas the wild-type behavior was to rip open the pod along its edge to expose the seeds either individually or several at a time (Frayne 2007). Additionally, one of the captive-reared birds released in 2004 used both the attacking and the ripping techniques. On several occasions we also observed a captive-reared bird attempting to open a pod without first severing the stem to detach it from the tree, as wild palila typically do. We observed another captive-reared bird foraging on the ground, which also would be unusual for wild palila.

Social Interactions and Breeding

The songs of some captive-reared birds sounded somewhat different from those of wild palila to experienced observers. Of the 21 birds released during 2003–2005, the calls or songs of three individuals (male C3.36, female C3.42, and female C5.56) seemed unusual. We were unable to characterize the vocalizations of birds in the 2009 cohort. The unusual vocalizations were heard long after birds had been released and exposed to wild palila. C3.36 was heard making calls similar to ʻapapane (*Himatione sanguinea*), and its "palila" calls sounded "raspy" at 51 days after release. The call notes of C3.42 sounded different 284 days after release, and strange calls were heard from C5.56 even 407 days after release.

The 2003 released birds quickly established social bonds within their cohort. Female C3.07 and male C3.44 were typically observed together after release, as were female C3.25 and male C3.36. On 4 February 2004, we observed C3.36 allofeeding C3.25. On 7 April 2004, C3.25 built a bulky nest, unlike the smaller, more compact nest typical of wild palila. The single egg laid in the nest was infertile (SDZICR unpublished data; see Chapter 2: Translocating Wild Palila). We found the nest 1.5 m high in a pūkiawe (*Leptecophylla tameiameiae*) shrub and 60 m downslope from Hack Tower 1 in a rocky area with few māmane trees.

We discovered one other pairing between captive-reared birds, female C4.48 and male C3.44, which in 2006 resulted in two fertile eggs that did not hatch (see Chapter 2: Translocating Wild Palila). More often, captive-reared males nested with wild, translocated females. C3.44 nested with T5-19 twice in 2007 and a fledgling was produced. C3.44 also nested with an unbanded female of unknown origin in 2008, when a fledgling was observed, and again in 2009, when another fledgling was observed. C3.38 nested with translocated female T4-06 in 2005, which resulted in two fledglings. C3.38 nested with translocated female T5-92 in 2007, but we found only two broken eggs in their nest. C5.55 was seen in 2007 courting a female that was the progeny of two translocated birds, but no nesting activity was observed.

In addition to courtship and breeding activity, we observed other social interactions among captive-reared birds. Male C3.44 and male C3.03 were seen foraging together on 5 July 2004, but we observed no interactions afterward. We also observed social activity between male C3.44 and male C3.36. On 20 September 2004, we observed calling between male C3.03 and female C3.42. Additionally, we recorded male C3.44 calling to female C4.45 from the 2004 release.

We observed several non-reproductive interactions between wild palila and the 2003 captive-reared birds soon after their release. On 20 April 2004, female C3.42 displayed open-bill gaping at a wild, translocated palila (sex unknown). The captive-reared bird flew away first but the wild bird quickly followed her. On several occasions, we noticed male C3.38 calling at, foraging in the same tree as, and flying with wild translocated palila. On 5 June 2004, we observed two wild palila allofeeding, with C3.38 in the same tree.

Throughout 2004 and 2005, we observed interactions between wild, translocated palila and three of the 11 captive-reared birds (Table 4.3) to assess their overall compatibility and the degree to which captive-reared birds might be integrated into a wild population. We observed the full range of interactions with some captive-reared birds interacting exclusively with other captive-reared birds, exclusively with wild palila, or with birds of each type. Five captive-reared birds were not seen interacting with translocated palila, but no translocated birds were available to interact with female C3.25. Male C3.38 and female C4.48 interacted exclusively with wild, translocated birds. We saw male C3.44 once with a wild palila (sex unknown), although he interacted with captive-reared birds on four occasions. We recorded wild, translocated palila calling or foraging with male C3.38 on 14 occasions from 17 June 2004 to 17 August 2005, and 21 different translocated birds were seen in association with this captive-released bird. On four occasions, C3.38 was observed with five or more translocated birds at one time. Also, five different translocated palila were observed with female C4.48, who was most often calling or foraging with one or two of the wild birds. Male C3.36 twice interacted with two translocated palila of unknown sex.

Discussion

Mortality soon after release was notable in 2003 and 2004. The two birds that died in 2003 were the oldest and youngest birds, suggesting a possible influence of age on the ability of birds to adjust to the stresses of the procedures or the new environment. Additionally, both birds had lost a substantial amount of weight since their release from the hack tower, and they died on a particularly cold night (U.S. Geological Survey unpublished data). Of the three birds

Table 4.3. Social interactions of captive-reared individuals with the mean number of observed (X_O) and available (X_A) translocated and captive-reared birds, 2004–2005. Total number of observations (*n*) includes solitary activity and interactions with unbanded or unidentified birds.

	Observation period			Translocated birds		Captive-reared birds	
Bird ID	Start	Stop[†]	*n*	X_O	X_A	X_O	X_A
C3.03	2-Jun-2004	10-May-2005	9	0.0	3.7	1.0	6.0
C3.25	27-Jul-2004	21-Aug-2004	3	0.0	0.0	0.0	0.0
C3.36	9-May-2004	4-Jul-2004	9	0.0	10.5	1.5	6.0
C3.38	8-May-2004	20-Jul-2005	30	2.8	25.0	0.0	5.1
C3.42	20-Aug-2004	2-Aug-2005	7	0.0	3.0	1.0	6.0
C3.44	22-May-2004	2-Aug-2005	15	1.0	10.4	1.0	7.1
C4.45	16-Feb-2005	16-Feb-2005	2	0.0	1.0	1.0	9.0
C4.48	28-Mar-2005	26-Apr-2005	7	2.0	31.8	0.0	8.2

[†] 2 August 2005 was the last day of possible observation.

that died during the 2004 release, one was apparently depredated by a cat, judging from bite marks on the transmitter. The causes of death of the two other 2004 birds that died were unknown. The carcass of one was heavily scavenged, but the body of the third was relatively intact and of normal weight. The SDZICR saw the depredated bird at the food pans regularly, but the two other birds did not visit the food pans after their release (T. Goltz, SDZICR, personal communication). Although māmane pods were not abundant at the time (see Chapter 16: Food Availability: Māmane Phenology), one of the birds exhibited no weight loss. The rapid disappearance of birds released in 2009, nevertheless, suggests food scarcity during a drought of exceptional length and severity (Banko *et al.* 2013). Additional research might be warranted to determine whether differences in māmane seed extraction techniques (Frayne 2007) affect the survival and reproductive success of captive-reared birds, especially when māmane pods are scarce.

The 2003 release birds did not demonstrate the post-release “flightiness” of some species when released into the wild (Tweed 2003). Rather, the birds stayed in close proximity to the hack towers. Approximately two weeks post-release, some 2003 birds started exploring the area around the hack towers. We observed that the captive-reared palila explored the area more once wild palila were translocated into the vicinity (see Chapter 2: Translocating Wild Palila). Although the captive-reared palila seemed to remain close to the hack towers, we found no significant difference between the home ranges of captive-reared and wild palila (see Chapter 12: Habitat Use, Home Range, and Movements).

The level of genetic variability of the first two cohorts of captive-released birds was only moderate. Since these were the first releases, the birds were conservatively chosen as nonessential to the long-term viability of the captive population (G. Witteman, University of Guam, unpublished data). Therefore, it was suspected that these released birds would not likely create a self-sustaining population due to their genetic homogeneity. This may partially explain why the egg collected from C3.25 was infertile. Nevertheless, fertile eggs were produced by female C4.48 and male C3.44, although they did not hatch. Moreover, captive-reared males produced offspring with wild females, suggesting that a high level of genetic variation might not be critical in the captive-reared population in order for releases of captive-reared birds to contribute to reintroduced populations containing wild birds.

The ultimate success of the captive-rearing program can only be determined through additional releases of birds. Several questions to consider are how productive captive-reared females can be and whether captive-reared females are attractive to and compatible with wild males, especially given differences in vocalizations between some captive-reared and wild palila. The acoustical environment of young palila in captivity may influence the quality of their vocalizations after their release to the wild. Of the birds that seemed to vocalize abnormally, one (C3.36) was parent-reared and two (C3.42, C5.56) were hand-reared. Of the birds that sounded normal to us, 17 were hand-reared and one was parent-reared; all seven birds of the 2009 release, whose vocalizations we could not characterize, were hand-reared. This indicates that hand-rearing may not have affected the vocal characteristics of released birds, and it remains to be determined whether the vocalizations of other bird species at KBCC may have influenced the vocalizations of the palila.

Long-term monitoring is critical to assessing the efficacy of reintroducing palila to its former range by releasing captive-reared birds. Important differences in behavior and survival between wild and captive-reared palila were revealed after the SDZICR 30-day monitoring period. Our results also suggest that research during captive rearing might improve the outcome of releases to the wild.

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SECTION II: DEMOGRAPHY AND BREEDING ECOLOGY

Preface

Understanding the demographic constraints that impede the palila's recovery is fundamental to developing restoration strategies. In this section, we report on the population trend since 1998 and the sharp decline in palila numbers due mainly to prolonged drought. These results were published in 2013 (Banko *et al.* in Biological Conservation 157:70–77), but a more detailed account is provided in Chapter 5. Sex ratio becomes an increasing concern as populations decline, and in Chapter 6 we describe how males become over-represented over time. Although palila are not exposed to mosquito-borne diseases due to the high elevation of their range, in Chapter 7 we report on our efforts to screen them for avian malaria, pox, and *Mycoplasma* bacteria.

A difficult problem to overcome in recovering many endangered species is their low reproductive capacity, and this is especially problematic for specialized species, such as the palila. In Chapter 8, we analyze the demographic characteristics of the breeding population with particular attention to the age distribution. We discuss the timing of breeding, productivity of breeding pairs, and nesting success in Chapter 9. The palila's habitat has been degraded by browsing, but the vegetation is also dynamic due to widespread regeneration of māmane following the culling of ungulate populations. We examine the characteristics of the vegetation associated with palila nests to understand how palila behavior is affected by habitat changes in Chapter 10. In Chapter 11, we describe the behavior of palila at their nests and their vulnerability to predators. These results were also published in 2003 (Laut *et al.* in Pacific Science 57:385–392).

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Chapter 7. Disease. Paul C. Banko, Carter T. Atkinson, Susan I. Jarvi, Luanne Johnson

Chapter 8. Breeding Demography. Paul C. Banko, Chris Farmer, Luanne Johnson, Colleen Cole

Chapter 9. Breeding Phenology, Productivity, and Nesting Success. Paul C. Banko, Chris Farmer, Luanne Johnson, Steven C. Hess, Colleen Cole, Steve J. Dougill, Kevin W. Brinck

Chapter 10. Nest Site Selection. Steve J. Dougill, Luanne Johnson, Chris Farmer, Paul C. Banko

Chapter 11. Behavior at Nests. Megan E. Laut, Elizabeth M. Gray, Paul C. Banko

5 POPULATION TRENDS AND RESPONSE TO ENVIRONMENTAL FACTORS

Paul C. Banko, Richard J. Camp, Chris Farmer, Kevin W. Brinck, David L. Leonard, Robert M. Stephens

Introduction

The decline of specialist species contributes substantially to the overall loss of global biodiversity (Clavel *et al.* 2011). Birds are useful indicators of biodiversity trends because they are widely distributed and their populations are relatively well monitored. Most globally threatened birds are tropical forest-dwelling species, but birds endemic to islands are most vulnerable to extinction (Birdlife International 2000). Since 1800, more than 90% of bird extinctions have occurred on islands. In the Hawaiian Islands 14 of 44 species of historically known forest passerines (songbirds) are extinct or have disappeared while 20 are listed as endangered, although 9 of these, most of which are Hawaiian honeycreepers (Fringillidae: Drepanidinae), have not been seen in decades (W. Banko and P. Banko 2009). The feeding specialists, species with unusual bills and relatively constrained or stereotypic feeding behaviors, have all disappeared or are in danger of extinction, whereas about one-third (10 species) of non-specialized passerines are still not considered threatened (W. Banko and P. Banko 2009). The majority of imperiled Hawaiian forest birds are Hawaiian honeycreepers, which are renowned for their extraordinary adaptive radiation from an Asian finch ancestor that arrived in the Hawaiian Archipelago less than six million years ago (Fleischer *et al.* 1998, Fleisher and McIntosh 2001, James 2004, Pratt 2005, Lerner *et al.* 2011).

The palila (*Loxioides bailleui*), a species of Hawaiian honeycreeper, is ranked among the 150 most critically endangered bird species (Birdlife International 2011), and its population and range are declining rapidly. The palila is the last honeycreeper species restricted to dry forest habitat, and it depends on the unhardened seeds that it extracts from the green pods of the māmane (*Sophora chyrsophylla*) for most of its food (Banko *et al.* 2002a, 2009). Māmane is an endemic, leguminous tree that was once more widely distributed but is now primarily found in dry montane and subalpine habitats on the islands of Hawaiʻi and Maui (Gagné and Cuddihy 1999). Specialization on māmane dramatically increases the palila's vulnerability to extinction, especially in the face of global climate change and multiple threats from invasive species. Palila cannot persist long where māmane is sparsely distributed or confined to a narrow band of elevation (van Riper *et al.* 1978, Scott *et al.* 1984) because the birds track seed pods as they ripen seasonally along an elevation gradient (Hess *et al.* 2001, Banko *et al.* 2002a, b). The range of elevation over which māmane occurs has been truncated by habitat destruction at both the lower and upper margins by nearly 200 years of browsing by introduced ungulates, which continue to degrade the remaining habitat (Banko *et al.* 2009). Another factor affecting palila habitat is drought, and a trend towards drier climatic conditions appears to be developing (Loope and Giambelluca 1998, Giambelluca and Luke 2007). Palila survival and reproduction decline during drought when māmane pod production is reduced (Lindsey *et al.* 1997, Banko *et al.* 2002a).

Range size is a powerful predictor of extinction risk among birds (Harris and Pimm 2008), and montane species are most vulnerable to the effects of climate change (Şekercioğlu *et al.* 2008, 2012). Palila are at risk from both factors because they are now entirely restricted to high-elevation habitats and they occupy one of the smallest ranges of any bird in Hawaiʻi (Gorresen *et al.* 2009). Historically, palila were found in woodlands dominated by māmane and naio (*Myoporum sandwicense*), another common endemic tree, on three of the five volcanoes of

Hawai'i Island: Mauna Kea, Mauna Loa, and Hualālai (Figure 5.1). Although palila were never reported historically below about 1,220 m elevation (Banko *et al.* 2002a), ancient bones reveal that they occupied coastal habitats on at least two other islands until disappearing sometime between Polynesian colonization around 800 years ago and the arrival of Westerners over 230 years ago (Olson and James 1982a,b; Burney *et al.* 2001). During Polynesian settlement, many Hawaiian passerines were extirpated presumably due to predation by the introduced Polynesian rat (*Rattus exulans*) and the destruction and modification of lowland habitats (Olson and James 1982b, Athens *et al.* 1992, James 1995). During Western settlement, habitat loss was accelerated by agricultural development, browsing and trampling by introduced ungulates, and invasion by weeds and pests (Cuddihy and Stone 1990, Pratt and Jacobi 2009). As a result of habitat loss and degradation, mostly due to cattle ranching and non-native feral ungulates, the palila's range has contracted to only 5% of its historical extent, and palila have disappeared from all areas outside the largest remaining forest fragment on the southwestern slope of Mauna Kea (Leonard *et al.* 2008, Banko *et al.* 2009).

Introduced ungulates are universal transformers of vegetation structure and composition and they can impact biodiversity in a number of ways, especially on islands (Spear and Chown 2009). Because protective adaptations against mammalian browsing are reduced or lacking in many plants endemic to remote oceanic islands (Carlquist 1974, 1980; Ziegler 2002; Lee *et al.* 2010), the structure and composition of plant communities are profoundly affected when ungulates are introduced (Loope *et al.* 1988, Cuddihy and Stone 1990, Merlin and Juvik 1992, Mueller-Dombois and Fosberg 1998, Wardle *et al.* 2001, Caujapé-Castells *et al.* 2010, Forsyth *et al.* 2010). Ungulates also impact the vegetation of islands near continents (Martin *et al.* 2010) and they limit populations of palatable trees and shrubs within their native continental ranges (Holmes *et al.* 2009). Habitat degradation by introduced ungulates has broadly affected Hawaiian bird communities (Henshaw 1902; Perkins 1903, 1913; Scott *et al.* 1986; van Riper and Scott 2001; W. Banko and P. Banko 2009; Pratt and Jacobi 2009) and has been the most important factor driving the palila's historical range contraction and population decline (Banko *et al.* 2009).

Since the early 1800s, cattle (*Bos taurus*), goats (*Capra hircus*), and sheep (*Ovis aries* and, more recently, mouflon [*O. gmelini musimon*] and their hybrids) have roamed widely through the palila's range, killing or damaging trees and shrubs, removing seedlings, and exacerbating erosion (Hartt and Neal 1940, Warner 1960, Kramer 1971, Juvik and Juvik 1984, Tomich 1986, Hess and Banko 2011). Cattle, goats, and sheep prefer māmane over non-native species (Giffin 1976, 1980), and long-term browsing has reduced the cover and regeneration of māmane as well as other tree and shrub species in palila habitat (Scowcroft 1983, Scowcroft and Giffin 1983). Large gaps created in māmane woodland by ungulates have been invaded by grasses and other weeds (Hess *et al.* 1999, Banko *et al.* 2009), greatly increasing the threat of fire (Thaxton and Jacobi 2009). Efforts to reduce ungulate populations during the 1930s and 1940s and since the 1980s have resulted in the episodic regeneration of māmane (Scowcroft and Conrad 1988, 1992; Hess *et al.* 1999). Nevertheless, forest recovery has been limited and intermittent because widespread browsing has continued (Banko *et al.* 2009, Hess and Banko 2011).

In addition to browsing ungulates, palila and other subalpine forest birds are threatened by a variety of other invasive species and climate change. For example, feral cats are major predators of birds on Mauna Kea, although rats play a secondary role (Pratt *et al.* 1997, Hess *et al.* 2004, Banko *et al.* 2009). Critical resources of palila are also exposed to many pressures

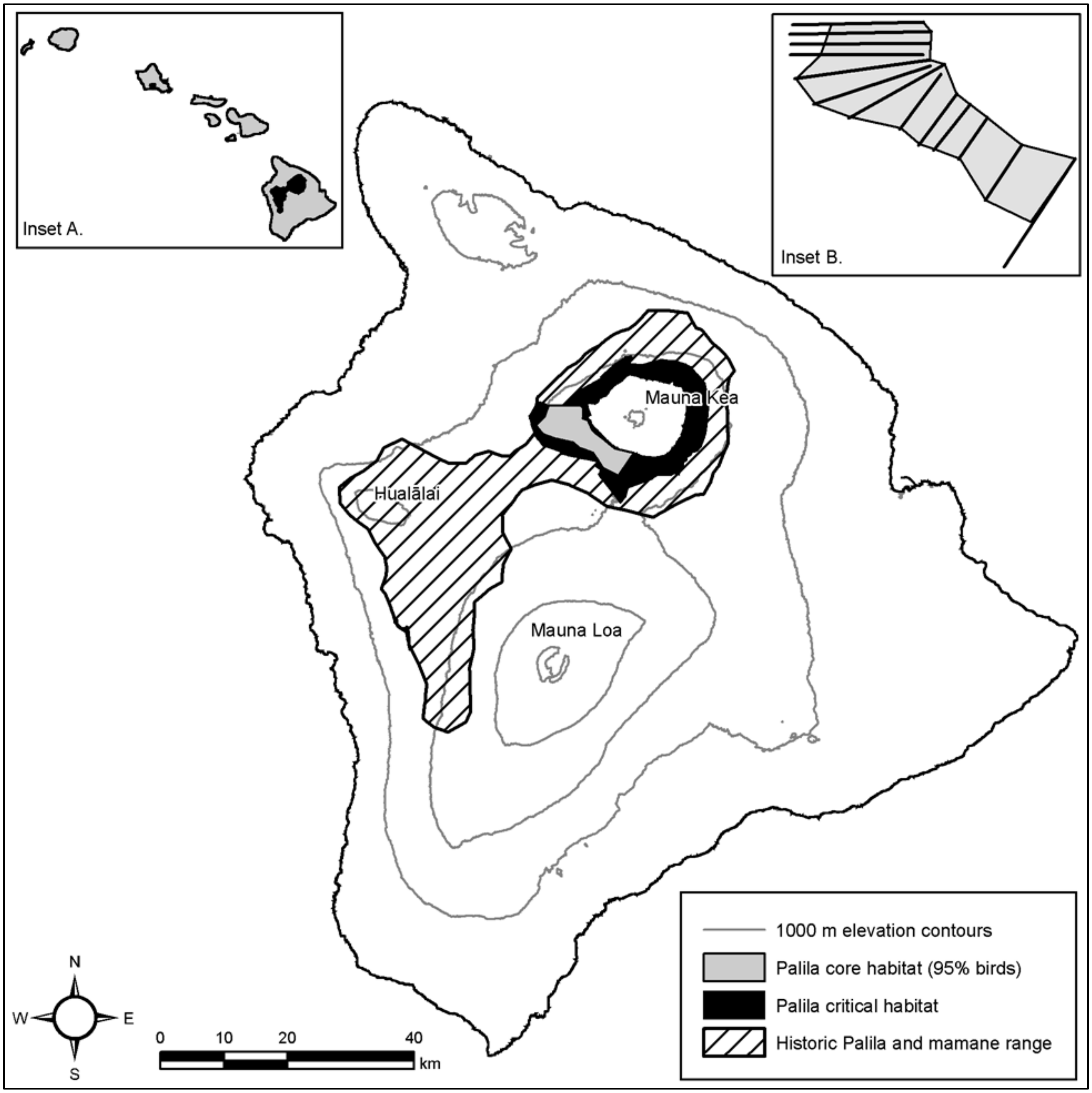

Figure 5.1. Historic range of the palila, current palila core habitat, Palila Critical Habitat, and range of māmane, which provides the primary food of palila. Once found in subalpine habitat on three volcanoes of Hawaiʻi Island, palila are now found only on the southwestern slope of Mauna Kea. Inset A shows the main Hawaiian Islands with the historic range of palila shown in black. Inset B shows the core palila habitat with survey transects.

from alien species. Not only does ungulate browsing reduce the availability of māmane seeds on individual trees and across the landscape (Banko *et al.* 2009), but caterpillars that are important foods of both nestlings and adults are vulnerable to parasitoid wasps, social wasps, and ants (Banko *et al.* 2002b, Brenner *et al.* 2002, Oboyski *et al.* 2004). Despite these problems, palila and other subalpine birds avoid the dangers of introduced avian malaria (*Plasmodium relictum*) and avian pox virus (*Avipoxvirus* sp.) because they range above the elevations where disease-transmitting mosquitoes (*Culex quinquefasciatus*) can exist or act as effective disease vectors (Atkinson and LaPointe 2009).

Malaria is a major factor limiting native Hawaiian bird populations in mesic and wet forests below about 1,500 m elevation (Warner 1968, van Riper *et al.* 1986, Atkinson and LaPointe 2009), but as nighttime temperatures continue to rise due to climate change (Giambelluca *et al.* 2008), mosquito-borne diseases are projected to increasingly threaten species living in what are now high-elevation, disease-free, but potentially suboptimal refugia (Benning *et al.* 2002, Atkinson and LaPointe 2009). Remnant populations of endangered birds are barely surviving in these areas due to other limiting factors (W. Banko and P. Banko 2009, Gorresen *et al.* 2009, Camp *et al.* 2010), and the incursion of disease could push their populations to extinction. Nevertheless, climatic trends indicate that the palila's dry, subalpine habitat will become even drier (Chu and Chen 2005, Cao *et al.* 2007, Giambelluca and Luke 2007, Chu *et al.* 2010), which might forestall an invasion of mosquitoes and diseases. On the other hand, a sustained drying trend also would likely affect vegetation structure and composition (Lohse *et al.* 1995, Loope and Giambelluca 1998, Juvik *et al.* 2011) and further reduce habitat carrying capacity. Climate change is expected to modify Hawaiian forest bird habitats, food webs, and the distributions of invasive threats in ways that are only recently being considered (Loope and Giambelluca 1998, Pratt *et al.* 2009). On Mauna Kea the effects of increased drought will be compounded because the forest is already stressed by browsing, pathogens, and competition from invasive weeds (Banko *et al.* 2009).

To assess how the subalpine bird community was responding to recent weather patterns, we evaluate population trends of palila and other passerines in relation to rainfall and drought since 1998, when annual surveys of all species began (Banko et al. 2013). This analysis is the first to include all passerines across a major portion of Palila Critical Habitat since the Hawai'i Forest Bird Survey program was initiated (Scott *et al.* 1986). Although we focus our attention on the palila due to its significance to conservation biology and policy, trends of the other species provide important context for understanding how species with divergent life histories respond to drought and habitat degradation. Data on weather conditions and on the ecology of palila, māmane, and naio were not collected continuously throughout the 14-year study period, but information overlapped sufficiently to allow us to explore major relationships. Additionally, earlier studies provide a basis for understanding how drought affects the breeding and survival of passerines (Lindsey *et al.* 1997, Pratt *et al.* 1997, Banko *et al.* 2002a) and the phenology and productivity of māmane and naio (Banko *et al.* 2002b). Although palila are the only birds that feed on māmane seeds, which contain high levels of potentially toxic alkaloids (Banko *et al.* 2002c), a number of other passerines forage in māmane for nectar and arthropods, including the ubiquitous, native Hawai'i 'amakihi (*Hemignathus virens virens*) and the widespread, introduced Japanese white-eye (*Zosterops japonicus*), both generalist foragers. Additionally, two species of Hawaiian honeycreepers, the 'i'iwi (*Vestiaria coccinea*) and 'apapane (*Himatione sanguinea*), visit subalpine Mauna Kea seasonally to feed on māmane nectar (Hess *et al.* 2001, Banko *et al.* 2002b). Palila and other bird species, notably the native generalist insectivore, Hawai'i 'elepaio (*Chasiempis sandwichensis*), and the introduced generalist frugivore-insectivore, red-billed leiothrix (*Leiothrix lutea*), also forage in naio, which is widespread on the southwestern slope of Mauna Kea (Scott *et al.* 1986). Although ungulates browse less on naio than they do on māmane, we have observed that drought impacts are more severe on naio than they are on māmane. Therefore, prolonged drought is likely to affect other passerines in addition to palila.

Our results provide insights about the roles of climate change and invasive species in shaping Hawaiian forest bird communities above the range of introduced mosquito-borne diseases, which have major impacts elsewhere (Scott *et al.* 1986). Our study also highlights the importance of increasing the carrying capacity of all forest bird habitats to help populations survive multiple environmental challenges.

Methods

Study Area

The survey area consisted of 64.4 km^2 of subalpine dry forest between 1,800 and 2,900 m elevation on the southwestern slope of Mauna Kea Volcano, Hawai'i Island (Figure 5.1). We refer to it as the "core" habitat or area of the species because it has supported over 95% of the palila population since standardized surveys began in 1980 (Scott *et al.* 1984). The climate is cool and dry. Annual mean temperatures range between 9 and 13°C; rainfall averages 511 mm annually and falls mostly during heavy winter storms, but cloud water intercepted by vegetation ("fog-drip") contributes additional precipitation (Juvik *et al.* 1993). The vegetation is dominated by two native tree species, māmane and naio (Hess *et al.* 1999, Banko *et al.* 2002b). Detailed research on the ecology of palila, other forest bird species, and the habitat has been conducted in the study area (van Riper *et al.* 1978; van Riper 1980a,b; Scott *et al.* 1984; Fancy *et al.* 1993, 1997; Lindsey *et al.* 1995; Jacobi *et al.* 1996; Pratt *et al.* 1997; Banko *et al.* 2002a, 2002b, 2009).

Survey Methods

The core palila population area was sampled with eight transects from 1980–1998. In 1998, five additional transects were established in the core area to improve population estimates, and surveys included all passerine species rather than a select group (Gray *et al.* 1999, Leonard *et al.* 2008). During 1998–2012, varying numbers of stations in core habitat have been annually surveyed on 12–13 transects (Table 5.1) using point-transect sampling methods (Johnson *et al.* 2006, Leonard *et al.* 2008, Camp and Banko 2012). Trained and calibrated counters estimated the horizontal distances from the station to all birds heard or seen during six-minute counts conducted before 11:00 HST during January–February.

Point-transect sampling data were used to calculate palila density estimates (birds/km^2) using the program DISTANCE, version 6.0, release 2 (Thomas *et al.* 2010). Right-tail truncation was set at 5% (87.0 m), the distance where the detection probability was approximately 10%. This procedure facilitates modeling by deleting outliers and reducing the number of adjustment parameters needed to modify the detection function. Selection of a detectability model was based on the lowest Akaike's information criterion corrected for small sample size (AICc; Buckland *et al.* 2001, Burnham and Anderson 2002). Candidate models were limited to half normal and hazard-rate detection functions with expansion series of order two (Buckland *et al.* 2001:361, 365). The uniform detection function was not considered because covariates of this dataset cannot be modeled. To improve model precision, sampling covariates were incorporated in the multiple covariate distance sampling engine of DISTANCE (Thomas *et al.* 2010). Covariates included observer and year of survey. Annual density estimates were calculated by post-stratifying data by year and location (inside or outside the core population) using the global detection function calculated across pooled strata. The 95% confidence intervals for the annual density estimates were derived from the 2.5th and 97.5th percentiles using bootstrap methods in DISTANCE for 999 iterations (Buckland *et al.* 2001, Thomas *et al.* 2010). Population estimates were the product of the density estimate times the area of the nominal core habitat

Table 5.4. Number of transects and stations sampled annually inside and outside the core palila area, 1998–2012.

	Inside core			Outside core		
Year	Transects	Stations	Counts	Transects	Stations	Counts
1998	12	355	357	14	186	186
1999	13	414	418	14	192	212
2000	13	418	424	17	224	224
2001	13	414	416	17	221	223
2002	13	416	417	20	270	271
2003	13	403	403	20	258	258
2004	13	397	397	18	240	251
2005	13	402	428	20	340	351
2006	13	386	398	20	323	356
2007	12	387	412	20	256	256
2008	12	386	432	0	0	0
2009	13	416	416	0	0	0
2010	13	415	420	0	0	0
2011	13	411	432	0	0	0
2012	13	486	909	20	360	360

(64.4 km^2). The model that best fit the distance histogram was a hazard-rate detection function with an adjustment term of a simple first-order polynomial expansion series, and the model included the survey year as an explanatory covariate.

To facilitate visual comparison of population patterns, we standardized the annual mean number of birds per station for each species by subtracting the overall mean and dividing by the standard deviation across all years (1998−2011). We then added a second order loess curve (span = 0.75) and applied a smoother to the data to illustrate trends (loess local regression smoother with span of 1). We tested for differences in the scaled pattern among species using the Kolmogorov-Smirnov test for goodness of fit.

Drought Index

To characterize the extent and severity of drought in the survey area, we used available data from the U.S. Drought Monitor website (http://droughtmonitor.unl.edu/). The Drought Monitor's severity categories are based on six major physical indicators and many supplementary indicators (Svoboda *et al.* 2002). The primary indicators are the Palmer Drought Severity Index and standard indicators of soil moisture, stream flow, precipitation, and remotely sensed vegetation health. Supplementary indicators include other widely used indices for monitoring drought, crop moisture, fire threat, evaporation potential, soil moisture, and other factors. An analytical tool developed for the Drought Monitor is the Objective Blend of Drought Indicators, which blends objective and subjective decisions about which measures to include and what weights to give them in the analysis. The basic premise is to automatically generate a consistent and replicable base layer of drought for an area of defined climate type.

We downloaded GIS (geographic information system) data that modeled the distribution of five qualitative categories of drought projected to occur on Hawaiʻi Island each week for the period January 2000−April 2011. To this dataset, we applied a GIS template to calculate the proportion of our study area covered by each category of drought, which included "abnormally dry," "moderate drought," "severe drought," "extreme drought," and "exceptional drought" in addition to "no drought." We then multiplied the proportional area by the rank (values 1–4 for drought and -1 for no drought) of the drought category that covered it to produce a score. Scores were combined into a composite score representing drought severity over the entire study area for each week, and these results were then averaged to produce monthly scores that were analyzed descriptively to characterize seasonal or annual environmental conditions.

Rainfall Patterns

Data available from the National Oceanic and Atmospheric Administration's National Climatic Data Center (NCDC; http://www.ncdc.noaa.gov/oa/ncdc.html) and the Hawai'i Division of Forestry and Wildlife (DOFAW) were analyzed to provide additional context for understanding bird population trends and to determine the degree to which the distribution of rainfall supported the results of the drought index. Due to substantial gaps or limited coverage in rainfall records that were available for the western slope of Mauna Kea, we selected Halepōhaku 111 rain gauge (19°46'N / 155°27'W) at 2,822 m elevation on the southern slope of Mauna Kea to evaluate long-term rainfall trends (1940–2010). Halepōhaku 111 is located at the Onikuza Center for International Astronomy near tree line at the southern periphery of our study area. We also used data from Pu'u Lā'au 102.1 rain gauge (19°50'N/155°36'W) at 2,268.9 m elevation in the heart of palila core habitat for limited historical patterns (1932–1977; data from NCDC) and for recent rainfall records (1997–2008; data from Hawai'i DOFAW). We included rainfall data for 1997 to provide the environmental context for the year preceding the 1998 (January) bird survey.

We excluded years with fewer than 11 months of data to calculate historical averages and to characterize months and years as wetter or drier than normal. We defined normal annual rainfall as falling within ± 0.5 SD of the mean, and rainfall values falling outside this interval were defined as: dry or wet (± 0.5–1.0 SD around the mean), very dry or wet (± 1.0–1.5 SD), and extremely dry or wet (± 1.5–2.0 SD). We did not use this system to classify monthly means; instead, we calculated historical (1940–1977) means to compare with recent monthly patterns of rainfall at Pu'u Lā'au (1997–2008) and Halepōhaku (1997–2010).

Impacts of Drought on Māmane Pod Production

To evaluate the impact of drought on māmane seed pod production during the palila breeding season, we estimated monthly pod abundance on 335 māmane trees in the survey area during April–August (the main breeding period of palila [Banko *et al.* 2002a]) of 2000 through 2004. We estimated monthly pod abundance by randomly selecting five māmane trees, each measuring at least 2 m in height and at least 2 m in crown width, at each of five elevations (2,200, 2,350, 2,500, 2,650, and 2,800 m) at point count stations along four randomly selected transects. Transects were the same ones used for surveying bird populations. We counted only pods that were potentially attractive to palila in that they were immature (still mostly green) and contained seeds that were mostly expanded (at least 3 mm).

Vegetation Structure and Browsing Impacts

During 1999–2001, we evaluated vegetation structure, māmane regeneration, and damage from sheep within the core habitat adjacent to bird survey stations. We measured tree canopy dimensions, counted saplings (0.2–2.0 m height), and recorded the incidence of browsed branch tips or bark stripping on 281 plots measuring 40 X 40 m.

Palila Nesting Effort

To evaluate the relationship between māmane pod abundance and the nesting effort of palila, we systematically searched for nests in the northern half of palila core habitat during the breeding seasons of 2000−2004. Teams of three to five searched for nests in every tree along belt transects that were at least 50 m wide and that varied in length from 900 to 6,450 m. The total area searched was 3.8 km^2 with effort distributed as follows: 53% (2.0 km^2) along transects also used for surveying bird populations and estimating māmane pod abundance, 34% (1.3 km^2) within two grids of transects in prime māmane forest (Pletschet and Kelly 1990), and 14% (0.5 km^2) within two grids of transects in mixed naio-māmane forest (see Chapter 9: Breeding Phenology, Productivity, and Nesting Success). Nests were counted if they contained fresh eggs or live chicks (active nests) or if they were empty but fresh in appearance and likely to have been built during the current season (inactive nests). Nests with weathered or debris-filled linings or nests that were beginning to disintegrate were not counted as nests of the year. Nest density was calculated from the total number of active and inactive nests of the year found within 25 m of transects.

Results

Palila Population Estimate and Trend

Estimates of the palila population during the 14-year period peaked at 5,952 (95% CI: 5,022−7,073) in 2003 then declined for eight consecutive years to 1,263 (938−1,613) in 2011 (Table 5.2, Figure 5.2). From 2003 to 2011, population estimates declined each year by an average of 586 ± 105.7 birds (mean ± SE; range 90−938) for a mean annual loss of 17% ± 3.5 (range 3−37%) or 79% overall. In 2012, the decline ended and the palila population was estimated to be 2,176 (95% CI: 1,749−2,640 birds; Camp and Banko 2012). Nevertheless, the average rate of decline from 2003 to 2012 was 519 birds per year for a 66% decline overall.

Table 5.2. Number of palila detected inside and outside the core palila area and annual population estimate with 95% confidence interval inside the core palila area, 1998−2011.

Year	# Detections inside	# Detections outside	Estimate	Lower limit	Upper limit
1998	313	2	4725	3833	5710
1999	388	1	5427	4505	6456
2000	234	14	3114	2500	3798
2001	345	4	4882	4002	5893
2002	339	9	4675	3905	5501
2003	439	7	5952	5022	7073
2004	371	9	5144	4326	5988
2005	315	1	4505	3725	5355
2006	271	16	3910	3150	4682
2007	210	3	3008	2450	3682
2008	186	0	2637	2116	3225
2009	189	NA	2547	1985	3143
2010	151	NA	1609	1245	1993
2011	119	NA	1263	938	1613

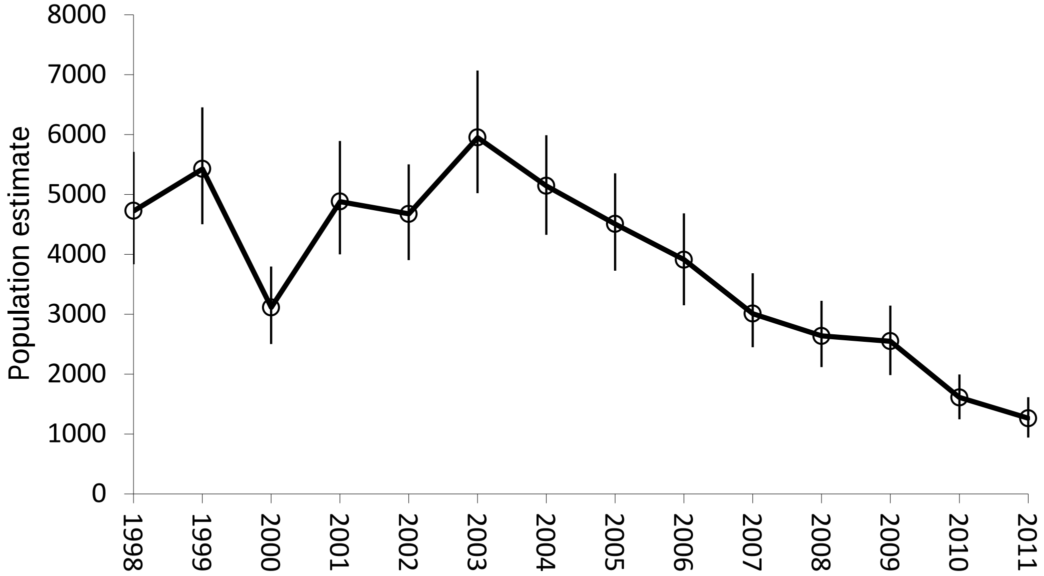

Figure 5.2. Annual palila population estimates and 95% confidence intervals derived from point-transect surveys since 1998, when, for the first time, all passerine species were surveyed instead of select species only and when survey effort was increased by adding new transects.

During the 1998–2010 surveys, palila were detected in 43.3 km^2 (67%) of the core area (64.4 km^2) with detections being broadly distributed in the northern portion of the core habitat and in a long tail across the upper elevations to the south (Figure 5.3). In 2011, palila detections were limited to 14.6 km^2 (23%) of the core habitat.

Community-wide Population Trends

We detected 20 passerine species over the course of the 1998–2011 surveys (Table 5.3). Nine species, including the sky lark (*Alauda arvensis*), were detected in all 14 years and were relatively widespread. We excluded the sky lark from further analyses because its conspicuous, aerial displays made it exceptionally detectable, and therefore inappropriate to compare with species that were mainly detected in trees and shrubs.

The most abundant species overall were Hawai‘i ‘amakihi (5.9 birds/station), house finch (*Carpodacus mexicanus*; 1.75 birds/station), and Japanese white-eye (1.14 birds/station; Appendix). The palila was the fourth most common species (averaging 0.66 birds/station) followed by the red-billed leiothrix (0.18 birds/station) and Hawai‘i ‘elepaio (0.13 birds/station). Low numbers of other species were detected in 1–13 surveys.

The melodious laughing-thrush (*Garrulax canorus*), northern mockingbird (*Mimus polyglottus*), and northern cardinal (*Cardinalis cardinalis*) were detected in 13 of the 14 years, although in very low numbers (Appendix). Four very rare or incidental species were detected in four or fewer years. The ‘akiapōlā‘au was detected only in 1998. The yellow-billed cardinal (*Paroaria capitata*) also was detected only in one year, whereas the nutmeg mannikin (*Lonchura punctulata*) was recorded in three annual surveys. The Japanese bush-warbler (*Cettia diphone*) was first detected on the 2006 survey, then intermittently on three later surveys. Of the six

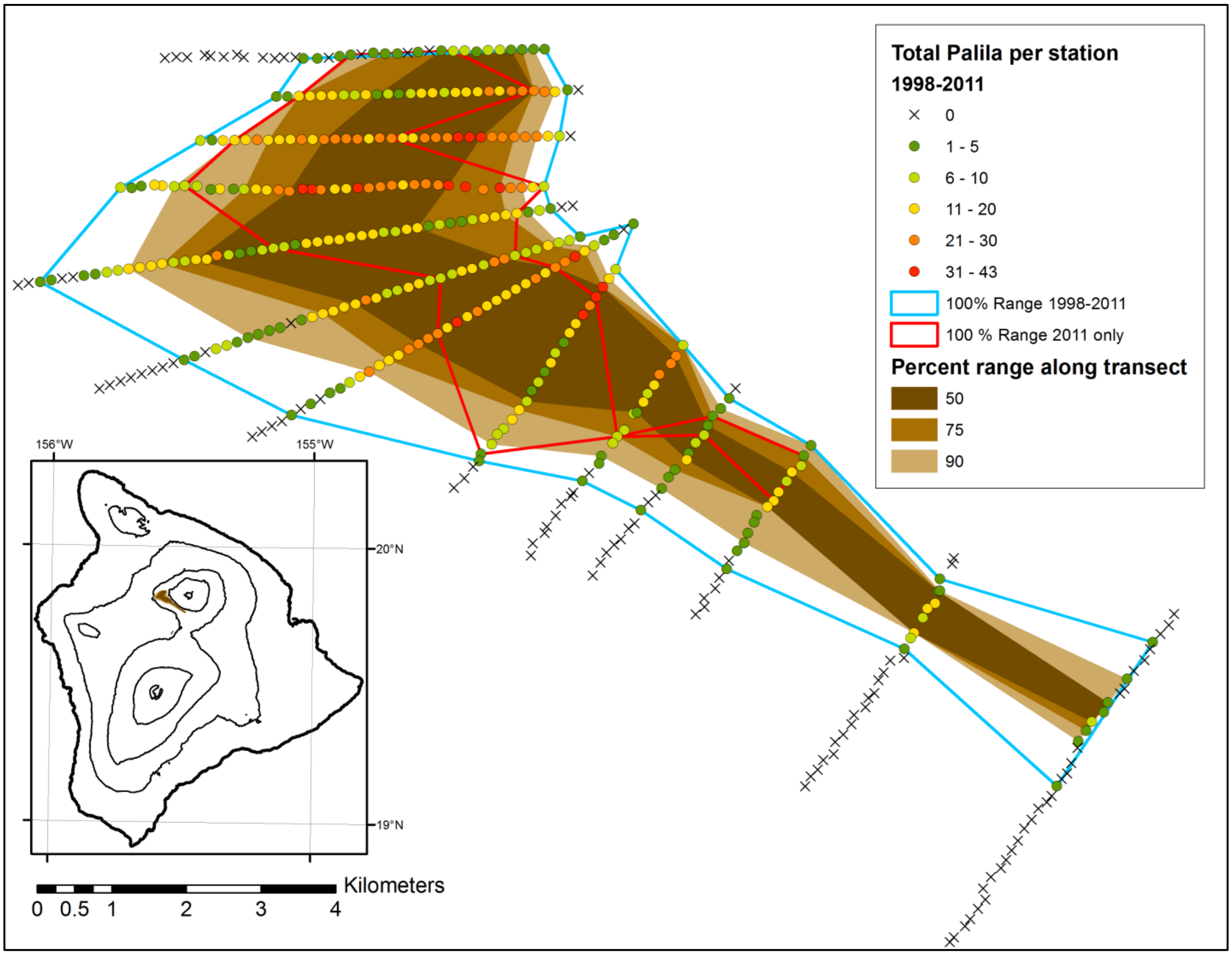

Figure 5.3. Distribution of palila detections in the core habitat on southwestern Mauna Kea, 1998–2011. Colored polygons represent the distribution of 90%, 75%, and 50% of detections at survey stations for all years combined. Polygons were constructed by identifying the station of each transect with 1-α/2 (i.e., 5%, 12.5%, or 25%, respectively) observations above it and the station with 1-α/2 observations below it. The area of each polygon was: 31.7 km^2 (90%), 23.5 km^2 (75%), and 16.6 km^2 (50%). The blue line defines the polygon containing all palila detections, and the red line defines the polygon containing only the 2011 detections.

most common species, population declines were evident for palila, Hawai‘i ‘elepaio, and Japanese white-eye, but annual estimates of the other species varied considerably and resulted in no apparent trend (Figure 5.4, Table 5.4). Declines in native seasonal visitors, ‘apapane and ‘i‘iwi, were the most notable trends among the less abundant species (Appendix).

Changes in the number of survey stations at which species were detected generally followed trends in species abundance (Table 5.4). Palila were detected at 34% of the stations (n = 373) surveyed in 1998, and 42% of stations (n = 421) in 2003, but only 18% of stations (n = 411) surveyed in 2011. In contrast, the proportion of stations occupied by Hawai‘i ‘amakihi declined very slightly from nearly 100% during 1998–2000 to 96% in 2011. The percentage of stations with Hawai‘i ‘elepaio also dropped somewhat overall, but especially so after 2004. Although ‘i‘iwi

Table 5.3. Passerines detected during surveys on Mauna Kea, Hawaiʻi, 1998–2011. Six endemic and 14 introduced species were distributed in 12 families, including the subfamily Drepanidinae (Hawaiian honeycreepers) in Fringillidae.

Family (subfamily)	Scientific name	Common name	Alpha code
ENDEMIC SPECIES			
Monarchidae	*Chasiempis sandwichensis*	Hawai‘i ‘elepaio	HAEL
Fringillidae (Drepanidinae)	*Loxioides bailleui*	palila	PALI
Fringillidae (Drepanidinae)	*Hemignathus virens virens*	Hawai‘i ‘amakihi	HAAM
Fringillidae (Drepanidinae)	*Hemignathus munroi*	ʻakiapōlāʻau	AKIP
Fringillidae (Drepanidinae)	*Vestiaria coccinea*	‘i‘iwi	IIWI
Fringillidae (Drepanidinae)	*Himatione sanguinea*	‘apapane	APAP
INTRODUCED SPECIES			
Alaudidae	*Alauda arvensis*	sky lark	SKLA
Sylviidae	*Cettia diphone*	Japanese bush-warbler	JABW
Timaliidae	*Garrulax canorus*	melodious laughing-thrush	MELT
Timaliidae	*Leiothrix lutea*	red-billed leiothrix	RBLE
Zosteropidae	*Zosterops japonicus*	Japanese white-eye	JAWE
Mimidae	*Mimus polyglottos*	northern mockingbird	NOMO
Sturnidae	*Acridotheres tristis*	common myna	COMY
Emberizidae	*Paroaria capitata*	yellow-billed cardinal	YBCA
Cardinalidae	*Cardinalis cardinalis*	northern cardinal	NOCA
Fringillidae	*Carpodacus mexicanus*	house finch	HOFI
Fringillidae	*Serinus mozambicus*	yellow-fronted canary	YFCA
Passeridae	*Passer domesticus*	house sparrow	HOSP
Estrildidae	*Lonchura cantans*	African silverbill	AFSI
Estrildidae	*Lonchura punctulata*	nutmeg mannikin	NUMA

were detected at few stations in the earlier surveys, they were not recorded at any stations during four of the last five surveys. Detections of even the widespread Japanese white-eye declined from 70% of stations in 1998 to 22% of stations in 2011. The numbers of stations where we detected house finch and red-billed leiothrix varied greatly from year to year with no obvious trend.

Drought and Rainfall Patterns

All categories of drought severity, including "no drought," were recorded during 2000–2010 (data not available for 1998–1999), but dry conditions were pervasive (Table 5.5). Drought conditions occurred during 98 (74%) of 132 months, with drought recorded in 52 of 54 months after June 2006. The longest period without drought was 14 months, which encompassed 2002, but other interruptions lasted only one to seven months. Drought was most severe in 2009, followed by 2010. Drought occurred in all months of the year but seemed on average more severe during summer and early fall (June–October).

Historical rainfall patterns at Puʻu Lāʻau and Halepōhaku were correlated during 1940–1977 (annual totals: $r = 0.417$, $P < 0.01$, 36 df; monthly totals: $r = 0.817$, $P < 0.01$, 10 df), although Puʻu Lāʻau rainfall was on average 71% that of Halepōhaku (1958, 1968, and 1969 excluded for

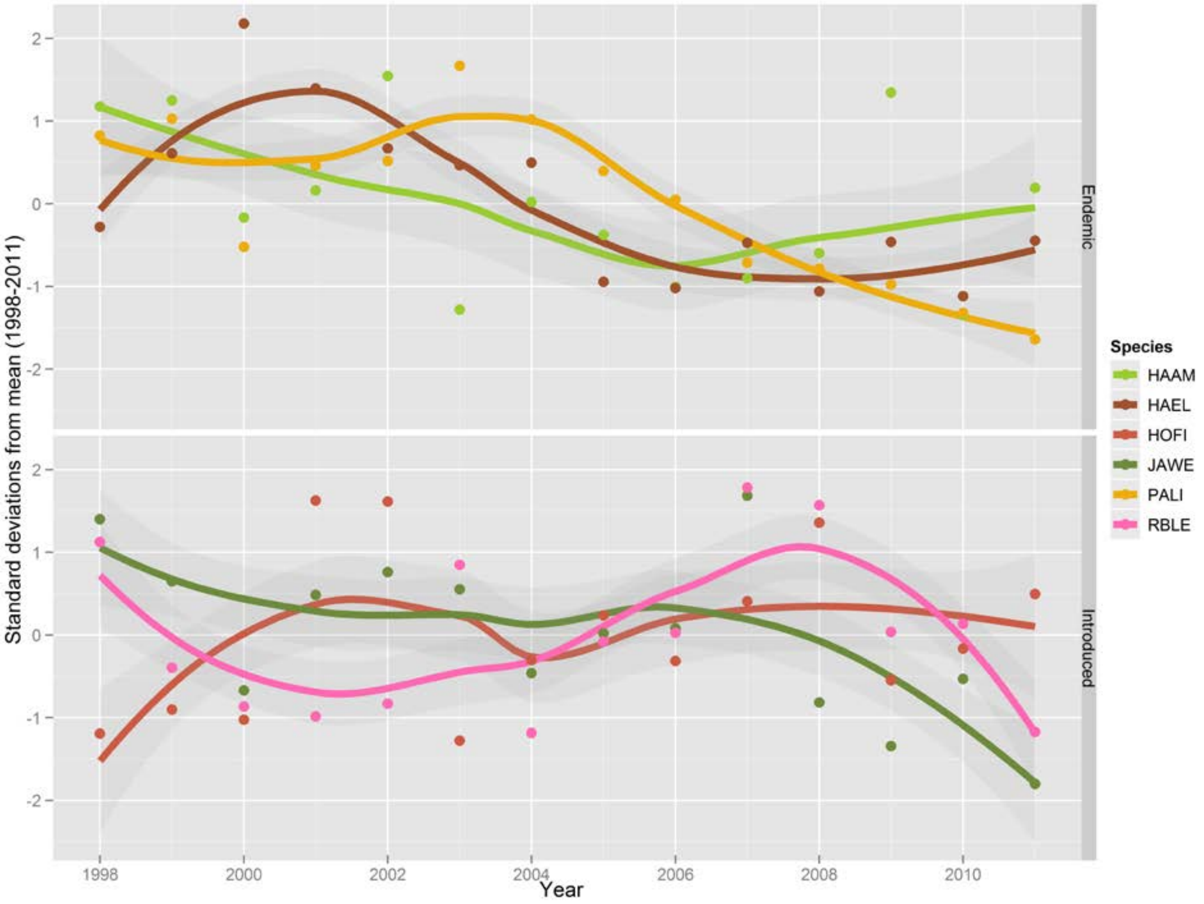

Figure 5.4. Population patterns of the six most abundant arboreal passerine species in core palila habitat, Mauna Kea, 1998–2011. Points are the standardized birds per station counted from 1998–2011. Lines are loess curves (second degree, span = 0.75). Birds are grouped into native species (Hawai‘i ‘amakihi [HAAM], Hawai‘i ‘elepaio [HAEL], palila [PALI]) or introduced species (house finch [HOFI], Japanese white-eye [JAWE], red-billed leiothrix [RBLE]).

both sites). Annual rainfall totals during 1940–1977 were highly variable (Table 5.6), and there was no clear trend at Halepōhaku (1940–2010; $r^2 = 0.001$, $P = 0.79$) or Pu‘u Lā‘au (1932–1977; $r^2 = 0.01$, $P = 0.50$). Since 1997, annual rainfall at both sites was lower than normal nearly twice as often as it was higher than normal when compared with the historical data, indicating that this period was unusually dry. At Pu‘u Lā‘au, 6 of 12 years were normal while 4 years were drier than normal and 2 years were wetter than normal (Table 5.7). In 14 years at Halepōhaku, only 3 years were normal and 7 years were drier than normal while 4 years were wetter than normal. The distribution of dry and wet years differed at each site, with all 4 dry years occurring before 2003 at Pu‘u Lā‘au and 5 of the 7 dry years occurring after 2003 at Halepōhaku. Overall, annual rainfall patterns provided weak and inconsistent support for the drought index.

Monthly patterns of rainfall agreed generally with the results of the drought index, but there were inconsistencies and mean monthly rainfall was variable at both sites, with values of

Table 5.4. Percent of stations occupied by species detected during annual surveys of the core palila habitat on Mauna Kea, 1998–2011, including mean percent occupancy (*n* = 5,846 stations surveyed). Trends in the percentage of stations occupied for each species (see Table 5.3 for key to species alpha codes) were based on the magnitude of change indicated by a best-fit linear model: decline or increase ≤25% (↔), decline ≤50% (↓), decline >50% (↓↓), local extirpation (X), insufficient data (NA). Occupancy increases >25% were not observed.

	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	Mean	Trend
ENDEMIC SPECIES																
HAAM	99.73	97.93	97.67	97.40	98.40	96.67	98.32	98.10	96.97	93.68	97.69	97.83	96.35	95.62	97.31	↔
PALI	34.32	33.87	27.51	28.84	33.64	42.28	41.59	30.64	30.81	24.59	23.15	23.61	22.38	17.76	29.64	↓
HAEL	7.24	9.91	15.62	13.71	11.90	11.64	9.86	4.28	4.80	7.26	5.79	6.99	4.14	7.06	8.58	↓↓
APAP	2.68	4.15	6.99	17.97	9.84	2.61	7.45	3.80	0.76	0.47	6.02	1.93	2.43	2.68	4.98	↓↓
IIWI	4.29	3.92	6.53	3.07	5.03	0	1.68	0.71	0.25	0	0	0	0.49	0	1.86	↓↓
AKIP	0.27	0	0	0	0	0	0	0	0	0	0	0	0	0	0.02	X
INTRODUCED SPECIES																
HOFI	50.40	56.68	48.72	78.96	70.02	52.26	57.45	55.58	66.92	62.30	72.22	60.24	59.12	65.94	61.20	↔
JAWE	70.24	60.60	47.32	63.59	64.53	63.90	52.40	51.31	59.60	73.30	41.90	32.53	47.20	22.38	53.63	↓
SKLA	36.46	37.56	46.85	45.39	40.05	26.13	40.14	44.18	49.24	57.85	55.32	35.66	21.41	36.74	40.93	↔
RBLE	19.84	7.60	4.66	3.55	5.95	15.68	1.68	9.50	11.11	19.20	23.84	10.12	11.68	1.95	10.45	↔
YFCA	4.83	7.60	2.80	4.96	11.67	5.23	3.85	2.85	9.85	2.81	1.62	3.13	6.57	1.70	4.96	↔
NOCA	5.90	8.76	5.83	2.84	5.49	2.14	5.29	2.85	6.31	3.98	11.11	5.06	0.97	0.49	4.79	↓
NOMO	2.41	1.61	0.47	0.47	2.06	1.66	1.20	1.90	1.52	2.58	2.31	1.45	0.49	0	1.44	↓
AFSI	0.80	0	0.23	0.71	1.60	1.90	0.24	0.24	2.78	1.41	0.69	0	0.97	0	0.83	↔
MELT	1.61	2.53	2.10	0.71	1.14	0.24	0.24	0.24	0.51	0.23	0.23	3.86	0.49	0	1.01	↓↓
JABW	0	0	0	0	0	0	0	0	0.25	0.47	0	2.89	0	0.97	0.33	NA
COMY	0.54	0.46	1.17	0	0	0.24	0.24	0	0.76	0.23	0	0	0	0	0.26	NA
HOSP	0	1.15	0.70	0.24	0.23	0.24	0	0.24	0	0	0	0	0	0	0.20	NA
YBCA	0	0	0	0	0	0	0	0	1.52	0	0	0	0	0	0.11	NA
NUMA	0	0	0	0	0.23	0.71	0	0	0	0	0	0	0.24	0	0.08	NA

Table 5.5. Index of drought for the core palila habitat on Mauna Kea, 2000−2010. Index values for each month are composites calculated from weekly projections available through the U.S. Drought Monitor website (see Methods) with -1 = no drought, 0 = abnormally dry, 1 = moderate drought, 2 = severe drought, 3 = extreme drought, and 4 = exceptional drought.

	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	Monthly mean
JAN	2.00	1.40	0.00	1.00	0.07	0.25	0.72	1.00	0.20	2.06	1.76	0.95
FEB	0.87	2.25	0.00	1.12	0.00	0.00	0.21	1.00	0.00	2.28	1.76	0.86
MAR	1.67	1.50	0.00	1.08	0.00	0.00	0.10	1.00	0.75	2.66	1.89	0.97
APR	2.00	0.00	0.00	1.67	0.00	0.00	0.00	1.00	1.00	2.83	1.97	0.95
MAY	2.00	1.16	0.00	0.72	0.00	1.13	0.00	0.97	1.00	3.00	1.97	1.09
JUN	1.97	1.76	0.00	1.79	0.00	1.50	0.00	1.73	1.00	3.00	1.65	1.31
JUL	1.96	1.94	0.00	1.05	0.00	1.00	0.50	2.00	1.48	3.00	1.57	1.32
AUG	1.87	1.50	0.00	2.10	0.00	0.00	1.00	2.00	2.14	3.00	1.57	1.38
SEP	1.96	1.00	0.00	1.91	0.80	0.00	1.00	2.00	2.14	3.00	1.57	1.40
OCT	1.20	0.20	0.00	2.39	1.75	0.00	1.00	2.00	1.25	3.00	1.57	1.31
NOV	0.74	0.00	0.00	2.97	1.00	0.00	0.00	1.25	1.25	1.89	1.59	0.97
DEC	0.17	0.00	0.00	0.93	1.00	1.00	0.75	1.00	1.74	1.89	1.47	0.90
Annual mean	1.53	1.06	0.00	1.56	0.38	0.41	0.44	1.41	1.16	2.63	1.70	1.12
Drought months	12	9	0	12	5	5	8	12	11	12	12	

Table 5.6. Historical monthly and annual rainfall (mm) means and standard deviation at Halepōhaku (HAPO) and Puʻu Lāʻau (PULA), 1940−1977. Sample size for each month was 35, except December at HAPO where it was 34.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	Annual
HAPO	94 ± 131.3	76 ± 78.9	89 ± 71.8	60 ± 78.3	30 ± 34.5	12 ± 19.4	28 ± 30.5	62 ± 81.9	32 ± 38.4	39 ± 32.8	72 ± 68.4	89 ± 86.0	680 ± 200.6
PULA	52 ± 58.4	45 ± 43.6	57 ± 54.9	52 ± 45.5	42 ± 43.8	18 ± 19.2	30 ± 27.8	39 ± 38.0	31 ± 29.2	27 ± 31.5	42 ± 43.2	41 ± 40.1	475 ± 174.5

Table 5.7. Distribution of recent wet and dry years at Halepōhaku (HAPO; 1997–2010) and Puʽu Lāʽau (PULA; 1997–2008) relative to historical (1940–1977) mean and standard deviation (SD; see Table 5.6). Normal annual rainfall was defined as falling within ± 0.5 SD of the historic mean, and rainfall values falling outside this interval were defined as: dry or wet (± 0.5–1.0 SD around the mean), very dry or wet (± 1.0–1.5 SD), and extremely dry or wet (± 1.5–2.0 SD).

	Years	Extremely dry	Very dry	Dry	Normal	Wet	Very wet	Extremely wet
HAPO	14	4	2	1	3	3	1	0
PULA	12	1	2	1	6	0	1	1
Combined	26	5	4	2	9	3	2	1

standard deviations sometimes exceeding mean values (Table 5.6). The driest months were June–October, which were 46% and 44% drier than November–May for Halepōhaku and Puʽu Lāʽau, respectively. Mean monthly rainfall at Puʽu Lāʽau during 1997–2008 (144 months) fell below historical means in 94 (65%) months, whereas 50 (35%) months were equal to or greater than their historical means (Table 5.8). Similarly, at Halepōhaku, monthly rainfall during 1997–2010 (161 months) was less in 115 (71%) months while 46 (29%) months were the same or greater than their historical means. The months of lowest rainfall were June–October, which were 39% and 52% lower than November–May for Puʽu Lāʽau and Halepōhaku, respectively (Table 5.6).

Effect of Drought on Māmane Pod Abundance and Palila Nesting

Drought affected the average number of pods per tree per month during 2000–2004, when data for estimating both the drought index and pod abundance were available. Contrasting the wettest and driest years, trees (n = 583) produced an average of 148 (± 16.7 SE) pods per month during the palila breeding season (April–August) in the drought-free year of 2002; but in 2003, the driest year, trees (n = 469) produced 76% fewer pods (35 ± 7.4 SE; Figure 5.5). Palila nesting effort increased somewhat with mean māmane pod abundance during April–August (Figure 5.6), but the high level of variability indicates that other factors also influenced nesting effort. In particular, nesting effort was high but pods were relatively scarce in 2000.

Habitat Structure and Carrying Capacity

We estimated that about 731,948 māmane and 730,516 naio trees populated the core area during 1999–2001. The mean cover of all tree species was 22.3%, of which māmane accounted for 7.8% and naio accounted for 14.4%. The mean height of 5,110 māmane trees was 3.83 m (1.27 m SD). We recorded māmane regeneration in 95.0% of plots, but high sapling densities (>100 per ha) occurred in only 28.5% of plots. Evidence of browsing or bark stripping by sheep was recorded in 59.1% of plots. The total number of palila counted per station during 1998–2011 was significantly correlated to the amount of māmane cover in adjacent vegetation plots ($P < 0.001$; correlation = 0.321; $r^2 = 0.103$; slope = 0.428 detections/percent cover).

Discussion

Decline of Specialist Species

The 79% decline in palila population estimates since 2003 is unprecedented in 32 years of monitoring (Banko *et al.* 2009). Also of concern is the 58% decline in the proportion of survey

Table 5.8. Distribution of wet and dry months at Halepōhaku (HAPO; 1997–2010) and Puʽu Lāʽau (PULA; 1997–2008) relative to historical (1940–1977) mean and standard deviation (see Table 5.6). Monthly rainfall totals of each year were compared to historical monthly rainfall means.

	HAPO (161 months)			PULA (144 months)		
	Drier	Same	Wetter	Drier	Same	Wetter
JAN	9		5	10		2
FEB	8		6	7		5
MAR	11		1	10		2
APR	12		2	10		2
MAY	10		3	8		4
JUN	7	1	5	7		5
JUL	11		2	6		6
AUG	13		1	8	1	3
SEP	8		6	6		6
OCT	8		5	5		7
NOV	9		4	8		4
DEC	9		5	9		3
TOTAL	115	1	45	94	1	49

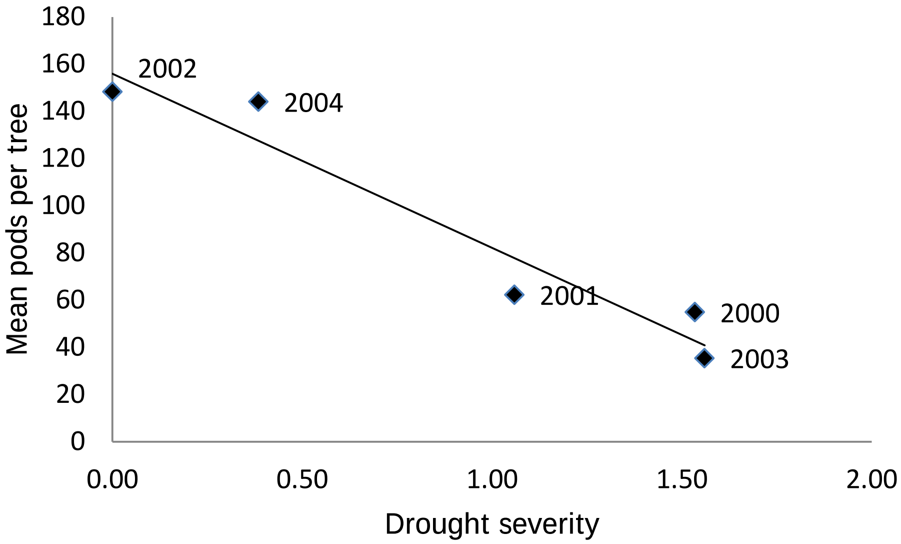

Figure 5.5. Linear relationship ($y = -73.772x + 155.9$, $r^2 = 0.9338$, $P = 0.007$) between mean māmane pod production per tree and drought severity. Māmane trees produced fewer pods in years when drought was more severe, as indicated by high annual mean drought index values. Monthly pod production was estimated for the palila breeding season (April–August).

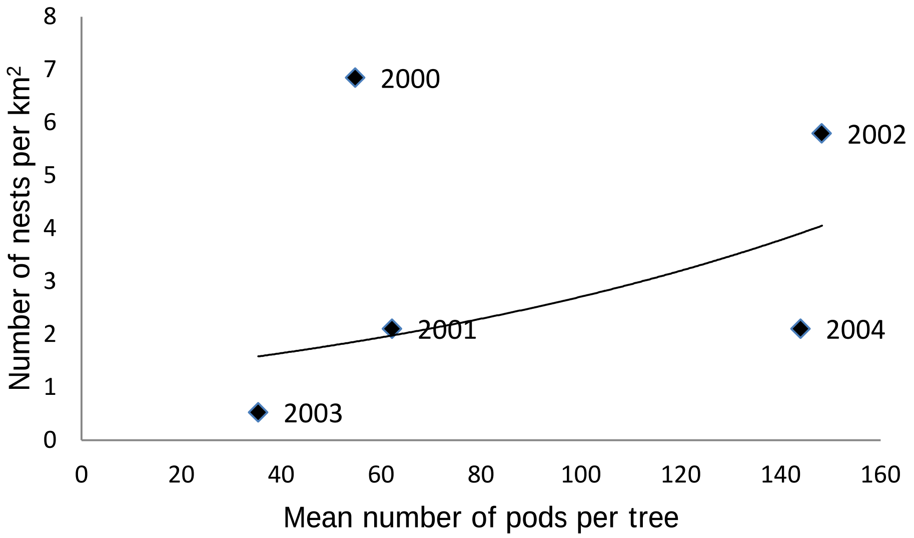

Figure 5.6. Exponential relationship ($y = 1.1794e^{0.0083x}$, $r^2 = 0.1861$) between number of palila nests per km^2 and mean number of māmane pods per tree during the palila breeding season (April–August).

stations with palila during 2003−2011. Palila were detected in <15 km^2 of habitat in 2011, underscoring their vulnerability to local catastrophes. At the present rate of decline, the species could be extinct very soon (Leonard *et al.* 2008), and even under improved environmental conditions, this diminished population will be slow to rebound due to low reproductive rates of wild birds and the limited ability to release captive-reared birds into the wild (Banko *et al.* 2009). Furthermore, absent effective management, relict populations of Hawaiian passerines have never been recovered and many that lingered at low levels for decades are now extinct or too rare to be detected (Banko *et al.* 2001, Gorresen *et al.* 2009).

The history of other bird populations on the southwestern slope of Mauna Kea is poorly known because early naturalists did not visit the area (Banko 1979−1990). Nevertheless, small populations of three endangered Hawaiian honeycreepers occurred there historically: Hawai'i creeper (*Oreomystis mana*), Hawai'i 'ākepa (*Loxops coccineus*), and 'akiapōlā'au (*Hemignathus munroi*). All three species are moderately to highly specialized insectivores and are typically associated with 'ōhi'a- (*Metrosideros polymorpha*) koa (*Acacia koa*) forest habitat, suggesting that subalpine māmane-naio forest may have always been marginal habitat for them, as it also may be even for the palila. The discovery of palila and many other Hawaiian forest bird bones in lowland and dry forest habitats suggests that modern ranges do not necessarily represent the full spectrum of habitats used by birds prehistorically (Olson and James 1982a).

A few Hawai'i creeper were observed in subalpine Mauna Kea from the 1940s into the 1970s (van Riper *et al.* 1978, Banko 1984a), but the species was not reported during or after the Hawai'i Forest Bird Surveys (Scott *et al.* 1986, Camp *et al.* 2009a). Hawai'i 'ākepa were observed in māmane-naio forest below Pu'u Lā'au in 1970 (Berger 1972) and 1971 (van Riper 1972) and were thought to be transients because of their strong association with 'ōhi'a-koa forest. Nevertheless, a specimen was collected near 2,285 m elevation on the northeastern slope of Mauna Kea in 1903 (Banko 1979, 1984b), suggesting that there may have been more than a passing association between the Hawai'i 'ākepa and subalpine māmane habitat.

More recently, the 'akiapōlā'au, which occurs in two isolated populations mainly in montane 'ōhi'a-koa habitats on Hawai'i Island (Gorresen *et al.* 2009), seems to have disappeared entirely from subalpine Mauna Kea and was last detected in our survey area in 1998. Local extirpations of the Hawai'i creeper, Hawai'i 'ākepa, and 'akiapōlā'au and the decline of the palila indicate that conditions on Mauna Kea are becoming unsustainable for a range of feeding specialists. In contrast, our surveys indicate that populations of generalist feeders, such as the Hawai'i 'amakihi, are relatively robust even in the face of formidable environmental challenges. Due to low reproductive capacity, reduced tolerance of ecological perturbations (P. Banko and W. Banko 2009, Şekercioğlu *et al.* 2012), and long-term, widespread habitat deterioration, this downward trajectory of specialists suggests that their recovery will be slow, even after effective management is applied.

Trends of Non-specialist and Uncommon Species

Despite their overall resiliency to disturbance, populations of some non-specialist species also declined on Mauna Kea, including the Hawai'i 'elepaio and the Japanese white-eye. Additionally, both species declined in the proportion of stations where they were detected, indicating that environmental stress is affecting some native and introduced generalists. Nevertheless, the generalist Hawai'i 'amakihi declined little in abundance or distribution, indicating a high degree of resilience.

Seasonal movement to the māmane forest by native nectar-feeders also declined during the survey period. 'I'iwi rarely visited southwestern Mauna Kea after 2006, which might have been due partly to the general scarcity of māmane flowers that we observed during the later surveys. The presumed source population of 'i'iwi residing in montane habitat on windward Mauna Kea (or possibly Mauna Loa) was marginally stable (closed-canopy forest) to declining (open-canopy forest), at least through 2007 (Camp *et al.* 2010). Therefore, we cannot rule out the possibility that a decline in numbers after 2007 also may have contributed to the drop in seasonal movement into our study area. Extensive 'i'iwi movements within montane forests on windward Mauna Kea have been noted, but individuals tracked to date have not been observed moving beyond this ecotype into subalpine habitats (Kuntz 2008). Therefore, the origin of 'i'iwi in the subalpine of Mauna Kea remains unknown. Although the windward 'apapane population followed the same marginally stable to declining trends observed for 'i'iwi (Camp *et al.* 2010), seasonal visitation to the subalpine māmane forest by 'apapane did not change significantly.

Small populations are expected to decline rapidly under deteriorating environmental conditions, although trends in small populations are difficult to detect (Gibbs *et al.* 1998, Gibbs 2000, Camp *et al.* 2009b). Nevertheless, our results indicated that small populations of the introduced melodious laughing-thrush, red-billed leiothrix, northern mockingbird, northern cardinal, yellow-fronted canary (*Serinus mozambicus*), and African silverbill (*Lonchura cantans*) persisted during the drought years. It seems unlikely that these populations were sustained solely by immigrants because potential source areas were also affected by drought. Nevertheless, some immigration apparently occurred during the drought because the introduced Japanese bush-warbler, a small insectivore associated more with dense understory vegetation (Foster 2009) than with dry woodland, established a small foothold in the study area, which is testament to the ability of some generalists to cope with harsh environmental conditions.

Impacts of Drought

The drought index provided relatively consistent evidence of the prolonged and extreme episodes of dry conditions that we observed on Mauna Kea. Although monthly rainfall patterns generally supported the results of the drought index, annual rainfall was less congruent, suggesting that localized storms distributed rainfall unevenly across the landscape. During normal to wet periods, for example, rain gauge totals at similar elevations on the southwestern slope of Mauna Kea varied by over 300 mm, although during drier periods they tended to vary less (Juvik *et al.* 1993). Nevertheless, rainfall patterns at Halepōhaku were more congruent with the drought index and our observations of wilted vegetation, dry soil, and the poor condition of the habitat in general. Although it was not measured, fog-drip can become the dominant form of precipitation under trees during periods of unusually low rainfall (Juvik *et al.* 1993), and fog-drip's contribution to canopy throughfall probably moderated drought impacts somewhat during our study.

The dry conditions that normally prevail in subalpine Mauna Kea (Juvik *et al.* 1993) influence the vegetation structure and composition (Hess *et al.* 1999), but the long-term effects of severe, multi-year drought on plant vigor, productivity, and recruitment are unknown. Long periods of abnormally dry weather could be expected to reduce tree cover and increase grass cover (Lohse *et al.* 1995, Loope and Giambelluca 1998), and monitoring would identify the extent to which māmane is being affected by drought.

The short-term effects of severe drought on passerine populations have been noted before on Mauna Kea (Lindsey *et al.* 1997), but results of our study allow consideration of the chronic drought impacts. Drought likely contributed heavily to the recent decline of palila, although effects on most other species were less pronounced or consistent over time. The palila population estimate peaked in 2003, just after the longest period of relatively normal weather during the study period, which was 14 months (November 2001–December 2002). The population declined each year thereafter, when drought conditions were interrupted on only six occasions, each lasting from one to seven months. Dry conditions were strongly associated with lower māmane pod production, and because palila survival and reproduction are reduced when pods are scarce (Lindsey *et al.* 1995, 1997; Pratt *et al.* 1997), fewer palila likely nested during the drought. Nevertheless, the relationship between nesting attempts and pod availability is weak (Banko *et al.* 2009), suggesting that age structure, sex ratio, or other factors also might influence annual nesting activity.

Among the common species that seemed most tolerant of drought conditions were those that forage mainly in grass and on the ground for seeds and insects: the house finch, yellow-fronted canary (*Serinus mozambicus*), and sky lark. Although Hawai'i 'amakihi may have avoided the graver consequences of drought by foraging in a variety of shrubs and trees, the Hawai'i 'elepaio and especially the Japanese white-eye fared less well. The decline in Japanese white-eye numbers could be the result of competition with the more abundant and somewhat larger Hawai'i 'amakihi during periods of low food availability and harsh environmental conditions.

Impacts of Browsing on Habitat Carrying Capacity

Despite the serious, immediate impacts of drought on palila demography, the most important, long-term manageable threat to the population is habitat degradation by feral sheep and mouflon sheep (Scott *et al.* 1984, U.S. Fish and Wildlife Service 2006, Banko *et al.* 2009). Over many decades, browsing has changed the structure and composition of montane and subalpine vegetation on Mauna Kea by removing seedlings, wounding saplings and trees, and reducing tree and shrub cover (Scowcroft 1983, Scowcroft and Giffin 1983, Scowcroft and Sakai 1983, Hess *et al.* 1999). Although browsing presumably depletes the non-structural carbohydrate reserves of all size classes of māmane trees, it is the seedlings, saplings, and small trees that should be especially vulnerable due to their shallow, less-developed root systems, greater proportion of leaf biomass, and reduced concentrations of non-structural carbohydrates (Niinemets 2010). On average, māmane measured during 1999−2001 were less than 4 m tall, suggesting that this relatively young population of trees should be highly susceptible to browsing, drought, and other stressors compared to a population of older, larger trees. Additionally, browsing likely reduces the tolerance of māmane and other species to the physiological burdens presumably imposed by drought, temperature extremes (Juvik *et al.* 1993), pathogens (Gardner and Trujillo 2001), and competition from invasive grasses and a variety of other weeds (Williams 1994, Banko *et al.* 2009). The ability of trees to tolerate multiple chronic stress factors is rare (Niinemets 2010); therefore, tree vigor and productivity should increase when browsing and other manageable sources of stress are alleviated.

Sheep have long been hunted on Mauna Kea, and during 1998−2010 nearly 11,000 sheep were removed from Palila Critical Habitat by a combination of public hunting (54%) and aerial shooting (46%; Hawai‘i DOFAW unpublished data). The impact of this program on the unmonitored population of sheep is unknown, but this level of removal has not prevented widespread, severe browse damage from continuing and it likely falls well below the annual rate of removal needed for eradication. Nevertheless, previous work (Scowcroft and Conrad 1988) and our vegetation surveys indicate that robust habitat recovery is possible in the absence of browsing. Although māmane crown cover was very low during 1999−2001, many of the trees we encountered were small (young) and saplings were widespread, if sparsely distributed. Even during the recent drought, māmane seedling density was observed to be 66.8 seedlings per ha only five years after browsers were eliminated from within a recently constructed ungulate exclosure, whereas 2.8 seedlings per ha were recorded outside the exclosure (Hawai‘i DOFAW unpublished data).

We can expect a long lag before palila fully benefit from forest recovery, given that palila are more common in areas with greater crown cover, taller trees, and a higher proportion of native plants in the understory (Scott *et al.* 1984). Our finding that palila detections increased with māmane cover confirms this relationship and establishes a basis for modeling the response of palila to improved habitat carrying capacity. For example, doubling the fraction of māmane tree cover from 7.8%, which is the mean for the core area, to 15.6% should yield 26% more palila detections during surveys. As tree size increases over time, palila detections should increase even more. Nevertheless, a rapid response to sheep eradication could be expected as lower tree branches re-sprout and canopy volume increases, yielding more food for palila and other birds (Banko *et al.* 2009). Given that most trees are less than 4 m in height and that browsing extends to at least 1 m, tree canopy volume could quickly increase by roughly 25% after removing sheep.

In the long-term, increased tree cover through ungulate eradication and habitat restoration will result in higher soil moisture through increased cloud water interception and canopy throughfall (Juvik *et al.* 1993) as well as less grass cover and reduced fire risk (Hess *et al.* 1999, Thaxton and Jacobi 2009). At a global scale, invasive grasses pose serious threats to ecosystems through competition with native vegetation for water and nutrients and by escalating fire risks through the accumulation of fine fuels and the promotion of grass-fire cycles (D’Antonio and Vitousek 1992). On Mauna Kea, invasive grasses and other weeds compete for water and nutrients with māmane and other native trees and shrubs, thereby adding to the stress of drought as well as suppressing regeneration and increasing fire threats (Williams 1994, Hess *et al.* 1999, Cabin *et al.* 2000). Reducing grass cover by promoting tree cover and potentially by the strategic application of herbicide could also, therefore, boost habitat carrying capacity. Results of our vegetation survey indicate that nearly 1.5 million māmane and naio trees are available to palila and other birds in the core habitat, yet many more trees are needed to sustain bird populations during prolonged drought.

Implications for Recovery

Although a variety of threats probably were responsible for the historical demise of rare, specialist species on Mauna Kea, factors other than drought and habitat degradation are likely unimportant or minor contributors to recent declines of palila or other bird species. Mosquito-borne diseases, which contribute heavily to native bird mortality at lower elevations, have little or no role in subalpine habitat (Banko *et al.* 2002a, 2002b, 2009). Predation, especially by feral cats, reduces palila nesting success, but predator control can substantially reduce impacts (Hess *et al.* 2004, Banko *et al.* 2009). Twenty-eight feral cats were removed from the palila core habitat during 1998–2000, and 51 were removed during 2002–2003 (Hess *et al.* 2009, see Chapter 36: Predator Management), but six years lapsed before a sustained control effort was implemented in 2009, which resulted in the removal of 78 feral cats through 2010 (Hawaiʻi DOFAW unpublished data). Although removing feral cats helps to protect bird nests on Mauna Kea, there is no indication since 1998 that bird populations have been responding to this management. Neither have there been recent invasions of alien species that might deplete important bird foods, although both parasitoid and predaceous wasps depredate caterpillars (Banko *et al.* 2002b, Brenner *et al.* 2002, Oboyski *et al.* 2004), and introduced ants are moving into the lower reaches of the subalpine zone where they threaten arthropods generally (Wetterer *et al.* 1998, Banko *et al.* 2002b, Krushelnycky 2007, U.S. Geological Survey unpublished data).

The disappearance of specialist feeders, most recently the ʻakiapōlāʻau, and the sharp decline in palila numbers underscore the urgency of protecting the forest bird community of Mauna Kea. Populations of specialist feeders have declined in subalpine Mauna Kea in recent decades, and the remaining specialist, the palila, is rapidly approaching extinction. The palila stands out among Hawaiʻi's many threatened forest bird species in that its ecology has been extensively investigated (Pratt *et al.* 1997; Banko *et al.* 2002a, 2009), and plans for their recovery have been developed from this sound scientific basis (U.S. Fish and Wildlife Service 2006). Nevertheless, all evidence points unmistakably to a collapsing population. In addition to the historical contraction of range, palila have not been detected outside the core area on the southern or eastern slopes since 2006, and the colony of palila experimentally reintroduced to the northern slope during 2003–2009 has also recently disappeared (Banko *et al.* 2009, see Chapter 2: Translocating Wild Palila). Without effective and timely intervention, demographic and stochastic factors may further impede recovery of the dwindling palila population. Priority action was long ago (1979) and repeatedly (1987, 1998) mandated by court order: permanently remove introduced browsing ungulates from Palila Critical Habitat (Juvik and Juvik 1984, U.S. Fish and Wildlife Service 2006). To help accomplish this goal, the original fence built in 1936 to protect Mauna Kea Forest Reserve from introduced ungulates is being replaced by an 82-km, ungulate-proof fence around most of Palila Critical Habitat, and funds are recently available for more effective eradication efforts (Banko *et al*. in press, 2014).

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Appendix. Birds per Station Index

Birds per station index by species detected during annual surveys in the core palila habitat on Mauna Kea, 1998−2011, including mean and total number of individuals. Endemic and introduced species are listed separately in order of abundance. Trends in annual mean number of birds per station for each species were based on the magnitude of change indicated by a best-fit linear model: decline or increase ≤25% (↔), decline ≤50% (↓), decline >50% (↓↓), local extirpation (X), insufficient data (NA). Population increases >25% were not observed.

	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	Mean	Total	Trend
								ENDEMIC SPECIES[1]									
HAAM	7.188	7.099	5.751	6.080	7.487	4.667	5.882	5.589	4.912	4.998	5.421	7.337	4.664	6.192	5.948	33,838	↔
PALI	0.842	0.896	0.545	0.783	0.776	1.043	0.892	0.748	0.682	0.492	0.444	0.451	0.367	0.290	0.661	3,861	↓↓
HAEL	0.107	0.164	0.266	0.217	0.167	0.154	0.156	0.067	0.063	0.096	0.079	0.101	0.058	0.102	0.128	746	↓↓
APAP	0.038	0.062	0.084	0.279	0.124	0.033	0.111	0.045	0.008	0.005	0.095	0.022	0.032	0.034	0.069	395	↓↓
IIWI	0.051	0.051	0.086	0.038	0.078	0	0.017	0.010	0.003	0	0	0	0.005	0	0.024	142	↓↓
AKIP	0.003	0	0	0	0	0	0	0	0	0	0	0	0	0	NA	1	X
								INTRODUCED SPECIES[2]									
HOFI	1.279	1.380	1.382	2.442	2.469	1.192	1.618	1.800	1.644	1.885	2.368	1.496	1.659	1.939	1.754	9,771	↔
JAWE	1.751	1.385	0.834	1.385	1.517	1.382	0.974	1.176	1.184	1.885	0.750	0.530	0.898	0.324	1.141	6,384	↓↓
SKLA	0.692	0.818	0.855	0.901	0.741	0.451	0.707	0.808	0.768	0.986	0.998	0.624	0.353	0.645	0.739	4,148	↔
RBLE	0.359	0.124	0.065	0.050	0.078	0.290	0.019	0.166	0.184	0.417	0.373	0.190	0.204	0.022	0.182	1,029	↔
YFCA	0.064	0.099	0.037	0.071	0.169	0.069	0.050	0.045	0.182	0.044	0.016	0.041	0.144	0.027	0.076	429	↔
NOCA	0.067	0.108	0.077	0.028	0.066	0.021	0.060	0.036	0.068	0.044	0.148	0.063	0.010	0.005	0.057	311	↓
NOMO	0.024	0.016	0.005	0.005	0.030	0.024	0.012	0.021	0.015	0.026	0.025	0.022	0.010	0	0.017	97	↔
AFSI	0.013	0	0.002	0.017	0.027	0.038	0.005	0.002	0.053	0.019	0.012	0	0.017	0	0.015	79	↔
MELT	0.024	0.028	0.026	0.007	0.014	0.002	0.002	0.002	0.005	0.002	0.002	0.048	0.005	0	0.012	69	↓↓
JABW	0	0	0	0	0	0	0	0	0.003	0.005	0	0.048	0	0.012	0.005	28	NA
COMY	0.008	0.007	0.026	0	0	0.002	0.002	0	0.008	0.002	0	0	0	0	0.004	23	NA
HOSP	0	0.014	0.009	0.007	0.009	0.002	0	0.005	0	0	0	0	0	0	0.003	20	NA
YBCA	0	0	0	0	0	0	0	0	0.015	0	0	0	0	0	0.001	6	NA
NUMA	0	0	0	0	0.002	0.007	0	0	0	0	0	0	0.005	0	0.001	5	NA

[1] AKIP (ʻakiapōlāʻau, *Hemignathus munroi*, Drepanidinae); APAP (ʻapapane, *Himatione sanguinea*, Drepanidinae); HAAM (Hawaiʻi ʻamakihi, *Hemignathus virens*, Drepanidinae); HAEL (Hawaiʻi ʻelepaio, *Chasiempis sandwichensis*, Monarchidae); IIWI (ʻiʻiwi, *Vestiaria coccinea*, Drepanidinae); PALI (palila, *Loxioides bailleui*, Drepanidinae)

[2] AFSI (African silverbill, *Lonchura cantans*, Estrildidae); COMY (common myna, *Acridotheres tristis*, Sturnidae); HOFI (house finch, *Carpodacus mexicanus*, Fringillidae); HOSP (house sparrow, *Passer domesticus*, Passeridae); JABW (Japanese bush-warbler, *Cettia diphone*, Silviidae); JAWE (Japanese white-eye, *Zosterops japonicas*, Zosteropidae); MELT (melodious laughing-thrush, *Leucodioptron canorum*, Timaliidae); NOCA (northern cardinal, *Cardinalis cardinalis*, Cardinalidae); NOMO (northern mockingbird, *Mimus polyglottos*, Mimidae); NUMA (nutmeg mannikin, *Lonchura punctulata*, Estrildidae); RBLE (red-billed leiothrix, *Leiothrix lutea*, Timaliidae); SKLA (sky lark, *Alauda arvensis*, Alaudidae); YBCA (yellow-billed cardinal, *Paroaria capitata*, Emberizidae); YFCA (yellow-fronted canary, *Serinus mozambicus*, Fringillidae)

6 SEX RATIO

Chris Farmer, Kevin W. Brinck, Paul C. Banko, Leayne D. Patch-Highfill, Susan I. Jarvi

Introduction

The study of sex allocation and factors affecting sex ratios is a significant component of evolutionary, population, and behavioral ecology (Fisher 1930, Charnov 1982, Frank 1990). At the population and species level, the evolutionary stable value for non-parthenogenetic species is unity; in other words, equal numbers of males and females (Fisher 1930, Charnov 1982). Further research has indicated sex allocation can depend on the mother's condition, the overall social context, and the relative gender-specific quality of the offspring the parents could produce (Trivers and Willard 1973, Gowaty 1991, Pen and Weissing 2002). The sex ratio of the offspring produced can also depend upon the age of the parent, as lifetime reproductive success and relative value of each potential offspring change through time (Weimerskirch *et al.* 2005, Husby *et al.* 2006). Advances in molecular techniques have made studies of avian sex ratios more feasible (Ellegren 1996, Griffiths *et al.* 1998, Jarvi and Banko 2000, Jarvi and Farias 2006). Numerous researchers have tested whether avian sex ratios were consistent with theoretical models, finding mixed evidence for adaptive sex allocation (Bensch *et al.* 1999, Cockburn *et al.* 2002, Laaksonen *et al.* 2004).

Sex ratios, and their biases, are also an important concern for conservation ecologists studying small or declining populations. Reliable sex determination, coupled with accurate demographic parameters, is necessary to assess population viability. A small population can be even more susceptible to geographical and behavioral factors (Gilpin and Soulé 1986, Lande 1993, Gerber 2006), or differential sex-based mortality, thereby changing the operational sex ratio (OSR); in other words, the number of males and females available for breeding at any one time (Emlen and Oring 1977). Steifetten and Dale (2006) demonstrated that a highly skewed OSR is the most likely factor limiting the population growth of ortolan buntings (*Emberiza hortulana*). A heavily male-biased OSR likely restricts reproduction in the cooperatively breeding rufous vanga (*Schetba rufa*; Eguchi *et al.* 2002, Asai *et al.* 2003). The adult sex ratio also correlates with general habitat quality (Fretwell and Calver 1970, Zanette 2001, Johnson *et al.* 2006) and population trends (Nadal *et al.* 1996, Wilkinson *et al.* 2002) for some avian species.

The palila (*Loxioides bailleui*) is a monogamous, highly endangered Hawaiian honeycreeper (Fringillidae: subfamily Drepanidinae) found only above 2,000 m on Mauna Kea Volcano, Hawai'i (Banko *et al.* 2002a). Before the arrival of people, palila populations were more widespread throughout the archipelago, extending down to sea level on some islands (Olson and James 1982, Burney *et al.* 2001). There are fewer than 1,700 birds remaining, mostly concentrated in 64 km^2 of māmane (*Sophora chrysophylla*) and māmane-naio (*Myoporum sandwicense*) forest on the southwestern slope of Mauna Kea (Leonard *et al.* 2008, U.S. Geological Survey unpublished data). Both sexes have delayed plumage maturation, attaining their adult plumage in the second prebasic molt, and these characteristics can be used to identify the gender and some age classes (Jeffrey *et al.* 1993). Lindsey *et al.* (1995) found a slight female bias in second-year birds, and a strong male bias in hatch-year and after-second-year birds, leading to 64% of the adult population being comprised of males. The success of captive breeding and release of palila (Lieberman 2005), as well as other endangered avian species, could depend upon balancing the species' OSR to minimize the effects of genetic drift and optimize long-term population persistence (Clout *et al.* 2002, Wedekind 2002).

Jarvi and Banko (2000) used PCR (polymerase chain reaction) amplification of CHD (chromodomain-helicase-DNA-binding protein) genes to determine sex in four species of Hawaiian honeycreepers in which the known sex was verified by necropsy. This study confirmed the accuracy of this PCR-based test for sex determination in honeycreepers. Subsequently, Jarvi and Farias (2006) verified the applicability of two other PCR-based methods in 12 endemic Hawaiian bird species, including palila. We used these established PCR-based tests to analyze the age-based sex ratio of palila, and to clarify uncertainties in the plumage identifications within some of the age classes. We compared the sex ratios based on plumage in palila captured during 1988–2007 with sex ratios based on PCR in a subset of this same population. We also re-examined whether morphological characteristics could be used to sex birds (Jeffrey *et al.* 1993). Additionally, because the palila is a long-lived passerine (Banko *et al.* 2002a), we were able to examine changes in the sex ratio within the after-second-year age class. The combination of PCR-based techniques and 13 years of demographic records allowed us to refine Lindsey *et al.*'s (1995) interpretation of the population sex ratio structure and for the first time, report the OSR for this endangered species.

Methods

Field Data Collection and Analyses

Using mist-nets, we captured and banded palila on Mauna Kea in all months from 1988 to 2007. The banding stations were set-up in areas of high palila density, and the nets were moved within and among years. We excluded pairs of birds that were banded at the nests. We determined the sex and age of captured individuals based on plumage (Jeffrey *et al.* 1993) and, when possible, on the presence of brood patches or cloacal protuberances. In 1994, we began collecting blood and feathers for DNA analyses of a subsample of these birds (see below). Adult male palila have a yellow head with a distinct napeline, containing <30% gray feathers (Jeffrey *et al.* 1993). Adult females have an indistinct or non-demarcated napeline, with yellow and gray feathers more extensively intermixed. These differences were scored (1−6) according to illustrations in Jeffrey *et al.* (1993). We categorized birds into hatch-year (HY), after hatch-year (AHY), second-year (SY), and after second-year (ASY) age classes. Presence of a complete or partial wingbar distinguishes HY and SY palila from ASY birds. Additionally, the lores and chin are darker than back feathers in ASY males, but lighter or the same shade in immature males and ASY females. The AHY class was comprised of birds whose ages could not be determined accurately due to molt during the fall months; these birds could have been either SY or ASY individuals (Jeffrey *et al.* 1993). The AHY birds' indeterminate plumage suggests that the standard sex differences might not apply. The sex of juveniles (HY) and nestlings is impossible to distinguish by plumage (Jeffrey *et al.* 1993); therefore, birds in these age classes were not sexed in the plumage dataset. Any birds assigned an "unknown" sex at the time of banding due to an inconclusive application of the sexing criteria were excluded from analyses, leaving a sample of 1,108 palila sexed only by their plumage and reproductive characteristics. When we estimated the OSR, we used all adult birds banded during this period that were definitively aged—even those with uncertain sexes (n = 1,534 birds).

The age class of birds was determined by their plumage (Jeffery *et al.* 1993), but when calculating each individual's age and its changes between classes, each bird was assumed to become one year older on 1 January. The initial ages were assumed to be 0 year for nestlings and HY birds, 1 year for SY and AHY birds, and all ASY birds were classified as 2 years at the time of first capture. This was done because of the protracted breeding seasonality found in Hawai'i. For example, HY birds were caught from March–December and SY birds were captured throughout the year. Because of the difficulty and imprecision in assigning an age to the AHY birds, they were excluded from most analyses.

We assessed the sex ratio of the ASY population over time by calculating ages for all birds captured at least twice, with at least one year between captures. All ASY birds fitting these criteria were included because of the low error rate in sexing ASY birds with plumage-based techniques (as shown later). Our calculation assumed that all ASY birds were in the 2–3 year category when first caught, so our analysis underestimated the number of older birds.

Sample Collection and Isolation of Genomic DNA

Tissue samples were collected during 1993–2007 from a subsample (*n* = 289) of the palila composing the total sample (*n* = 1,108). Breast feathers were the tissue source for DNA extraction from 208 adults; blood or muscle were the tissue sources for 67 samples; and muscle tissue was collected from 14 failed embryos that died in the egg. Tissues were stored as described in Jarvi and Banko (2000). DNA extractions for the muscle or blood tissues were carried out using DNeasy^{TM} Tissue Extraction Kit (QIAGEN$^{®}$) following the manufacturer's protocol. Feather samples were extracted using either the DNeasy Tissue Extraction Kit or QIAamp DNA Micro Kit (QIAGEN$^{®}$) extraction protocol for Forensic Case Work Samples. Larger feather pulps were individually sliced or chopped with disposable blades to allow complete digestion of the tissues. Additional minor modifications to the manufacturer's protocol are described in Patch-Highfill (2008).

Eggs (*n* = 14) were opportunistically collected when found in inactive nests during May–July each year. A total of seven eggs came from two successful and three unsuccessful nests (mean clutch = 2 eggs). Nestlings (*n* = 38) were sampled during May–November from 23 nests (18/22 fledged a chick, one nest with no data; mean clutch = 1.9). A separate study of 557 active nests indicated that mean clutch size for palila is 1.9 eggs, 49% of eggs (*n* = 764) do not hatch, and 47% of chicks (*n* = 387 nestlings) do not fledge (U.S. Geological Survey unpublished data), suggesting that the egg and chick samples analyzed by PCR were not abnormal.

Amplification of CHD Genes

The CHD-based primers used in this study were evaluated for accurate and reliable sex determination in 12 endemic and 8 alien Hawaiian bird species and were shown to provide a consistent, reliable means of sex determination in palila (Jarvi and Banko 2000, Jarvi and Farias 2006). PCR reactions were carried out in 25 μl volumes as described in Jarvi and Farias (2006) using primer sets P2/P3 (Griffiths *et al.* 1996), P2/P8 (Griffiths *et al.* 1998), or both. Positive control samples (one known male, one known female) were included in each PCR test along with a negative control (using dH_2O instead of template DNA). All products were analyzed by electrophoresis in 2% agarose (3 parts Nuseive to 1 part SeaKem Agarose, Lonza) gels stained with ethidium bromide. The 288 samples were evaluated at two different times. Initially, 231 samples were tested multiple times (average 3.4 PCRs/sample) with either primer set P2/P8, P2/P3, or both. An additional 57 palila samples were later examined to increase statistical power, and were evaluated using the P2/P3 primer set with the modification that samples were subjected to a hot start at 94°C for 4 minutes rather than 30 seconds. Five samples from the earlier round of testing were re-analyzed in the second round to validate results from the second round of testing. Replicate PCR reactions combined with the use of multiple primer sets on samples ensured the accuracy of the PCR sex assignment. Overall there was a 98.3% agreement among the samples with a positive sex identification, with 5% of all samples tested by PCR being indeterminate.

Statistical Analyses

We looked for evidence of an uneven sex distribution within age classes by calculating the two-tailed binomial probability of a 1:1 sex ratio given the observed sex ratios using both the plumage- and PCR-based methods. Birds sexed by PCR were not included in our set of plumage-sexed birds to maintain two independent samples. We tested whether there were different sex ratios across the age classes within each sexing method using χ^2 test of homogeneity. Female palila may begin breeding as SY birds, that is, in the first nesting season following the year of their hatching, but males do not breed for at least another year, when they have entered the ASY class (Pratt *et al.* 1997, U.S. Geological Survey unpublished data). Therefore, we considered the OSR to be the ratio of SY females plus ASY females compared to ASY males. Because SY birds were difficult to sex accurately using plumage characteristics, the OSR was calculated using sex ratios that were determined by PCR and this ratio was applied to the total numbers of birds in each age class from the entire banding dataset of SY, AHY, and ASY individuals (*n* = 1,534 birds) to calculate the OSR for the adult population.

We also examined the sex ratio of known-age birds for evidence of sex-biased mortality. Birds that had been captured more than once, with the captures separated by at least one year, and that were sexed by PCR analysis, plumage, or reproductive status, were used to calculate sex ratios across age categories. Because of potential uncertainties in sexing the SY birds, we limited this analysis to ASY birds. We pooled the ASY birds into four age-based categories with approximately equal numbers of individuals (3, 4–5, 6–10, 11–17 years old) for our examination of sex-based differential mortality.

We tested whether our results were a function of a sex-based capture bias or were due to an actual biological bias in sex ratios using a binomial test to compare the initial sex ratio of ASY captures to the sex ratio of these birds when recaptured within 60 days. Sixty days was chosen to minimize the effects of mortality and the species' known seasonal movement patterns (Hess *et al.* 2001, Banko *et al.* 2002b). ASY birds were the only age class with reliable identifications and sufficient recaptures within that time window. The pool of confidently sexed ASY palila consisted of 151 females and 253 males, giving an initial sex ratio of 0.60 F:M. If there were a sex-biased capture rate, the sex ratio of recaptured birds should be significantly different from 0.60, assuming each sex's recapture rate was the same as its initial capture rate, and that there was no sex-based difference in mortality. Conversely, similarity in the sex ratios of initially captured and recaptured birds would argue against a sex bias in the capture rate but would support an actual skewed sex ratio in the population. We also attempted to test for differential capture probabilities using banding data combined with re-sight observations of banded birds for all birds in a comprehensive Barker model (Barker 1999, White and Burnham 1999), but the model never converged and was uninformative, therefore we were unable to explicitly test for sex-specific capture probabilities using our entire banding dataset (U.S. Geological Survey unpublished data).

Analyses were conducted with Microsoft Excel (Microsoft Corporation 2003). The experiment-wise level for statistical significance was set at *P* = 0.05.

Results

Capture frequencies of different age classes varied seasonally (Figures 6.1a, 6.1b), but patterns were similar for plumage and PCR sexing techniques. Nevertheless, a substantial error rate in the plumage-based sexing of the SY age class complicated the interpretation of these results (discussed below). Across all age classes, both the plumage- and PCR-based sex ratios indicate

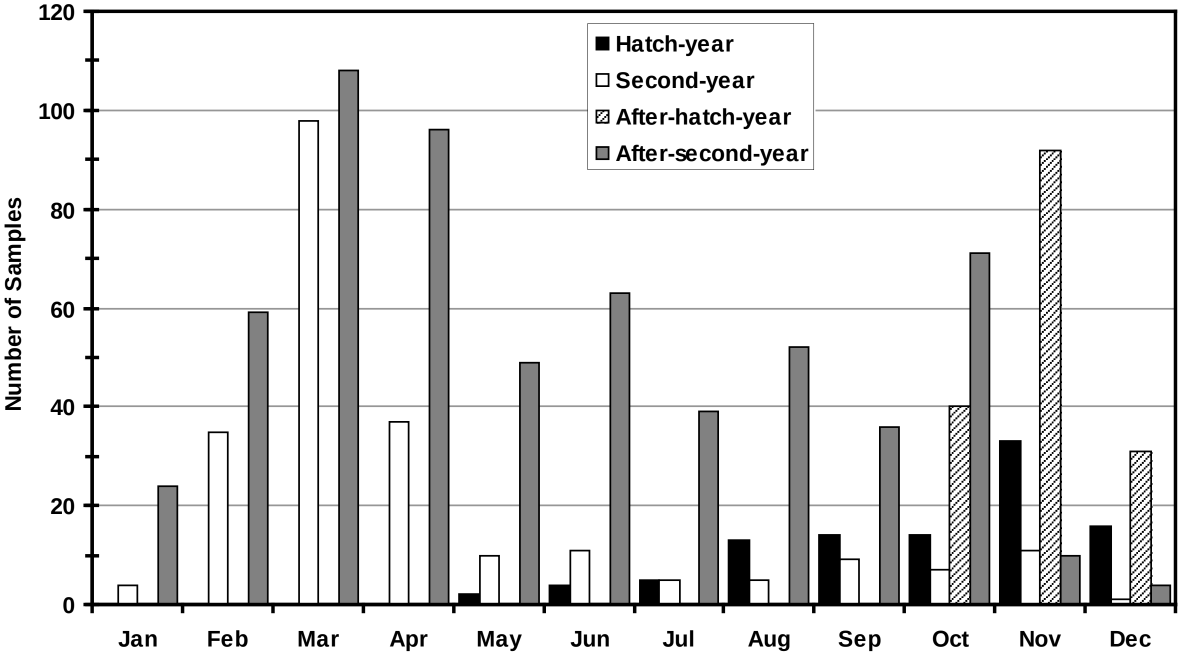

Figure 6.1a. Palila sampled for plumage-based sexing from the western slope of Mauna Kea Volcano, Hawai'i, during 1988–2007.

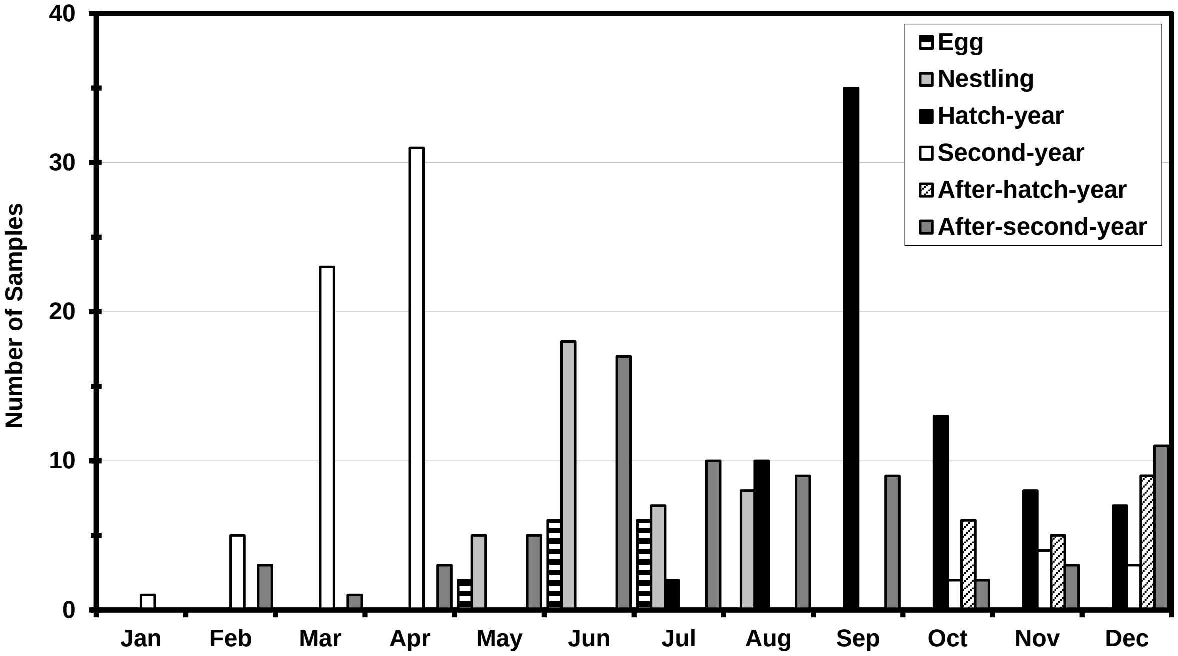

Figure 6.1b. Palila sampled for PCR-based sexing from the western slope of Mauna Kea Volcano, Hawai'i, 1993–2007. None of these birds are included in Figure 6.1a. Note the different scales on the y-axis between 6.1a and 6.1b.

a male bias: 61% and 54% male, or 433F:675M and 134F:155M, respectively (Table 6.1). We analyzed the sex ratio of the combined plumage and PCR sex ratios in each month for the HY, AHY, SY, and ASY age classes, and found that there was a strong male bias across all months (Figure 6.2; $\chi^2_{11} = 75.7$, $P < 0.001$). The result was the same whether we examined SY and ASY together, or only the ASY individuals (all $P < 0.01$).

Table 6.1. PCR-based (1993–2007) and plumage-based (1988–2007) sex ratios for palila. Probability values are from two-tailed binomial tests for an even sex ratio within each age class. Both techniques indicated a significant difference among age classes (PCR $\chi^2_3 = 8.7$, $P = 0.03$; plumage $\chi^2_3 = 110.6$, $P < 0.001$).

	PCR-sexed birds				Plumage-sexed birds			
Age group	Female	Male	Sex ratio (F/M)	*P*	Female	Male	Sex ratio (F/M)	*P*
Egg	8	6	1.33	0.3953	–	–	–	
Nestling	21	17	1.23	0.3136	–	–	–	
Hatch-yr	34	41	0.83	0.2443	39	62	0.63	0.0140
After-hatch-yr[1]	4	16	0.25	0.0059*	50	113	0.44	<0.0001*
Second-yr	38	31	1.23	0.2352	176	57	3.09	<0.0001*
After-second-yr	29	44	0.66	0.0503	168	443	0.38	<0.0001*
TOTAL	134	155	0.86	0.1197	433	675	0.64	<0.0001*

[1] Adult birds that could not be accurately aged

* Significant at an experiment-wise type I error rate of 0.05 across the multiple statistical comparisons

PCR analysis of embryos and nestlings (N) indicated a female bias in the primary sex ratio, but the difference was not significant (embryos = 8F:6M, binomial test $P = 0.39$; nestlings = 21F:17M, $P = 0.31$). Assuming an even sex ratio, we found no within-clutch sex bias in nests with two nestlings ($n = 15$ clutches, $\chi^2_2 = 0.1$, $P = 0.97$). Both techniques indicated a male bias in all post-fledging age classes except the SY birds. Binomial tests for an even sex distribution revealed five cases (one PCR-based, four plumage-based) where the sex ratio was significantly different from unity (Table 6.1). Sex ratios differed significantly across age classes whether using plumage determination ($\chi^2_3 = 110.6$, $P < 0.001$) or PCR ($\chi^2_3 = 8.7$, $P = 0.034$). Although a male bias was found in the HY and AHY classes using PCR, the difference was only statistically significant for AHY birds (Table 6.1). Because of the difficulty in determining whether AHY birds were SY or ASY, they were excluded from further age-based analyses. Although both sexing methods revealed an excess of females in the SY age class, the PCR-based results were not statistically significant and the plumage-based dataset was compromised by classification errors. The two techniques also indicated a male bias in the ASY age class, which again was statistically significant only for the sample sexed by plumage.

We tested the plumage-based sex identification technique by comparing those individuals that were sexed using both methods. Comparing the results for the 155 post-hatch-year birds that

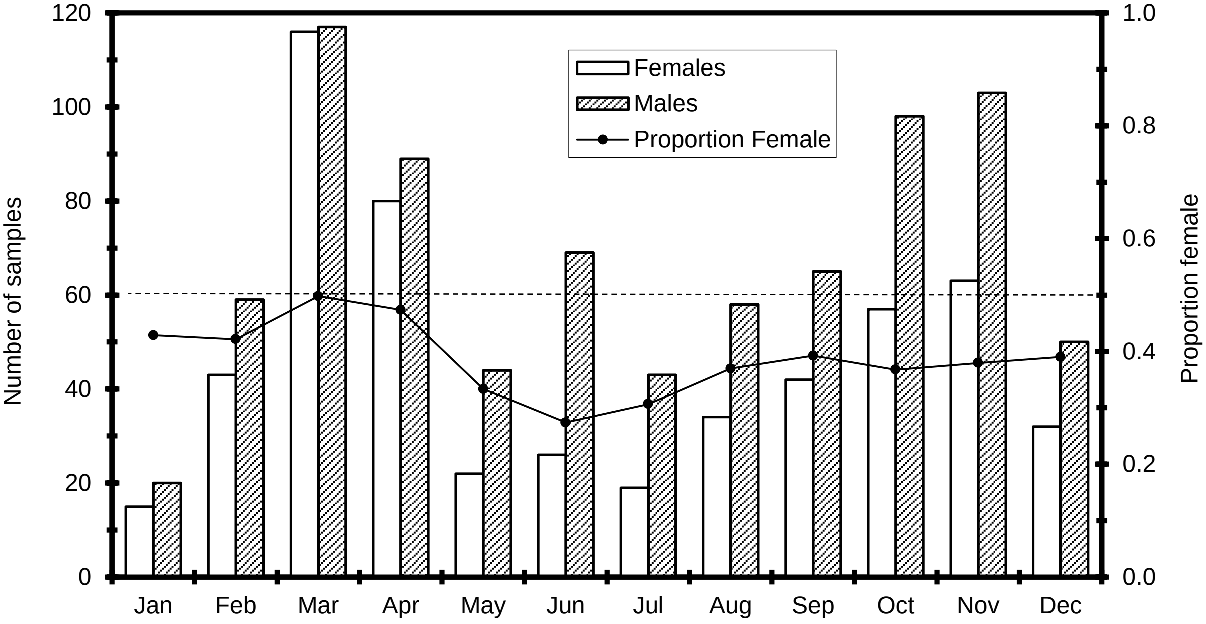

Figure 6.2. All known-sex, post-fledging palila from both the plumage- and PCR-sexed datasets, 1988–2007; including 164 SY birds sexed solely by plumage characteristics.

were definitively sexed in the field, the PCR determinations contradicted plumage determinations for 18% (16/87) of males and 3% (2/68) of females, with the majority occurring in the SY age class (Table 6.2). Additionally, of 80 palila that could not be assigned a sex by plumage characteristics, 36 were female and 44 were male based on PCR analysis.

Because our results indicated that plumage-based sex determination of SY birds could be inaccurate, we applied the PCR results to our larger banding dataset to estimate sex ratios at the population level. To address the error rate in plumage-sexed SY birds (Table 6.2), our OSR calculation applied the sex ratio data from the PCR analysis to calculate the age class proportions in the entire banding dataset. The PCR analysis indicated that the SY class was 55% (38/69) female and the ASY class was 40% female (29/73). When these proportions were applied to the entire banding dataset of SY, AHY, and ASY individuals (n = 1534 birds) we obtained an OSR of 1.05 (578F:552M; 95% CI = 0.62–1.60).

We used a binomial test to determine whether differences in sex ratios might reflect a sex-related bias in capture rates rather than a real sex bias in the population. From an initial sample of 404 confidently sexed ASY palila (151 females, 253 males; F:M = 0.60), we recaptured 10 females and 20 males (F:M = 0.50) 60 days later. The difference in the initial and recapture sex ratio was not statistically significant (P = 0.74). Even when the recapture time window was relaxed to 90 days, the sex ratio (13 females, 21 males; F:M = 0.62) was not significantly different (P = 0.52), indicating that males outnumbered females.

Because we assumed that all ASY birds were 2–3 years old when first caught, our analysis underestimated the number of older birds. Nevertheless, there were twice as many males as

Table 6.2. Error rates of palila sexed by both plumage and PCR. The field error rate is the proportion of individuals within each plumage-based age and sex class that were mistakenly sexed (e.g., based upon plumage there were 48 SY females, but PCR indicated that 14 were males, so the field error rate was 0.29 for this age-sex class). The classification error rate is the proportion of PCR-sexed individuals that were mistakenly sexed by plumage (e.g., based upon PCR there were 36 SY females, two were classified as males by plumage, so the classification error rate was 0.06).

	Sex determined by DNA		
Sex determined by plumage	Female	Male	Field error rate
SY Female	34	14	0.29
SY Male	2	13	0.13
Classification error rate	0.06	0.52	
AHY Female	4	1	0.20
AHY Male	0	15	0
Classification error rate	0	0.06	
ASY Female	28	1	0.03
ASY Male	0	43	0
Classification error rate	0	0.02	
Overall Female	66	16	0.20
Overall Male	2	71	0.03
Classification error rate	0.03	0.18	

females in the ASY age class, and this proportion did not change as age increased ($\chi^2_3 = 3.1$, $P = 0.43$; Table 6.3).

Measurements of the 69 PCR-sexed SY palila show that there are significant, albeit subtle, differences in the plumage and morphology of males and females. While statistically significant, differences in wing chord (males = 87.6 mm, females = 85.3 mm; t = -4.0, $P < 0.001$), tarsus (males = 25.2 mm, females = 24.3 mm; t = -3.9, $P < 0.001$), bill length (males = 12.7, females = 12.3; t = -2.5, $P = 0.01$), and weight (males = 38.0 g, females = 36.1 g; t = -3.3, $P = 0.001$) are too similar to enable observers to distinguish gender in the field. The most substantial difference was in the nape score, with SY males having a more distinct napeline (mean = 3.5) between their yellow head and gray back compared to females (mean = 5.3, Mann-Whitney $U = 888.0$, $P < 0.001$; see Jeffrey *et al.* 1993 for plumage scoring details). These nape values are similar to the values of Jeffrey *et al.* (1993), 3.14 and 5.3 respectively, which are the basis for sexing birds in the field. Therefore, we cannot improve upon the established criteria for identifying gender in the field.

Discussion

After verification of the CHD-based sexing techniques in palila and other Hawaiian honeycreepers (Jarvi and Farias 2006), we determined the sex of 289 palila, and compared these sex ratios with ratios based on plumage in a larger dataset of 1,108 palila. Both PCR and plumage techniques showed a significant difference in sex ratios among age classes, with a strong tendency towards males in the adult age class (ASY), where males outnumbered females by ≥50% in both sample types. We found no statistically significant sex-based difference in the recapture probability of adult birds, similar to Martin *et al.* (1995), suggesting the different

Table 6.3. Sex distribution of birds captured multiple times. The age is based on the age at the last time of capture and underestimates the number of older birds because it assumes that all ASY birds were two-years-old when initially captured. The sex is based upon the overall classification from PCR analysis or plumage characteristics. Analysis of age-specific mortality used four bins with approximately equal numbers of birds (3, 4–5, 6–10, and 11–17 years).

Age	Female	Male	Female:Male	Total
3	7	18	0.389	25
4	10	11	0.909	21
5	6	10	0.600	16
Subtotal	16	21	0.762	37
6	1	2	0.500	3
7	1	4	0.250	5
8	1	5	0.200	6
9	1	3	0.333	4
10	2	4	0.500	6
Subtotal	6	18	0.333	24
11	2	3	0.667	5
12	1	2	0.500	3
13	0	1	0	1
14	0	0	–	0
15	0	0	–	0
16	0	0	–	0
17	0	1	0	1
Subtotal	3	7	0.429	10
TOTAL	32	64	0.500	96

capture probabilities reflect a true bias in the population. The transition from an even sex ratio to a male bias after individuals begin breeding is typical for most birds (Breitwisch 1989, Liker and Székely 2005, Donald 2007). Both methods of sex determination indicated parallel shifts in sex ratios from HY (tendency towards males) to SY (female bias) to ASY (male bias) as Lindsey *et al.* (1995) reported previously. We found that sexing SY birds using the plumage-based technique alone is subject to a high error rate. Given the age- and sex-specific field error rates (Table 6.2) and plumage sample size, approximately 8 designated males and 51 females (25% of the entire SY plumage sample) were incorrectly sexed using the plumage technique. However, the adjusted numbers (133 female and 100 male SY birds) were still significantly female biased ($P = 0.02$). The nape was the most differentiated visual characteristic between genders in the SY class, similar to findings of Jeffrey *et al.* (1993), with the other morphological traits being uninformative for gender discrimination. Both our PCR- and plumage-based techniques revealed a significant male-bias and moderate error rate in the AHY class (Tables 6.1 and 6.2), suggesting that difficulty in aging an individual is not correlated with difficulty in sexing that individual.

Although there was no statistically significant change in the sex ratios, and by extension the mortality rates, of ASY birds caught multiple times (Table 6.3), the sex ratio of the overall ASY population shifted slightly toward males when the results of both methods were combined (Table 6.1; 197F:487M, 0.405). This suggests that delayed breeding in subadult males is a function of competition for females (e.g., Lack 1968, Rohwer *et al.* 1980, Studd and Robertson 1985). Females presumably suffer higher mortality related to breeding, while males generally have greater longevity (Banko *et al.* 2002a, U.S. Geological Survey unpublished data). The large male bias in the ASY birds could also explain the basis for helping behavior, where unmated ASY males (12/13 observations of helping) assist in feeding females and related offspring (Miller 1998, Patch-Highfill 2008).

The global population in 2014 of fewer than 2,200 palila is limited to 64 km^2 on Mauna Kea (Camp *et al.* 2014), which makes this species prone to extinction from environmental, demographic, and genetic stochasticity (Gilpin and Soulé 1986, Gabriel and Bürger 1992, Lande 1993, Frankham 1995, Melbourne and Hastings 2008). Rainfall patterns are highly variable on Mauna Kea, and droughts are frequent (Western Regional Climate Center 2007), leading to variation of nearly 500-fold in the abundance of the palila's primary food, māmane pods (U.S. Geological Survey unpublished data). Environmental effects on resource availability (Byholm *et al.* 2002) and offspring survival (Husby *et al.* 2006) have been demonstrated to affect avian sex ratios, and given the conditions on Mauna Kea, there could be similar impacts on palila sex ratios. Palila are relatively long-lived, and if environmental variability affects sex ratio, then several consecutive sub-optimal years could impact palila demography and behavior. Avian species that the International Union for Conservation of Nature (IUCN) classifies as vulnerable, endangered, or critically endangered (the palila is classified as critically endangered; BirdLife International 2012) also have more male-skewed ratios than non-threatened species with the magnitude of the skew increasing as the species status deteriorates (Donald 2007). Palila population estimates have been declining drastically since 2003 (Leonard *et al.* 2008, Banko *et al.* 2009), so there is the possibility that the male-bias found in our 1988–2007 data could be becoming more extreme.

Engen *et al.* (2003) demonstrated that fluctuations in sex ratio increase the overall demographic variance. Such fluctuations could decrease the long-term viability of the palila population. Over the twenty years of our study the OSR, which included SY females but not SY males, was 1.05, but the composition of the actual breeding population, and therefore the effective OSR for any specific year, is unknown. Annual reproduction is highly variable on Mauna Kea (Pratt *et al.* 1997, Banko *et al.* 2002a, U.S. Geological Survey unpublished data), and nesting surveys suggest that many SY females, and even ASY females and males, do not breed in many years. Although it is unclear how the different age classes respond to drought, differential sensitivity to environmental conditions could magnify fluctuations in the OSR, leading to an increase in demographic variation and increased susceptibility to extinction (Gabriel and Bürger 1992, Lande 1993, Melbourne and Hastings 2008).

Knowledge of the sex ratios and understanding the transitions between age classes is critical for calculating survival rates, conducting population viability analyses, and planning conservation strategies for endangered species (Dennis *et al.* 1991, Lacy *et al.* 1992, Lindsey *et al.* 1995, USFWS 2006). The palila is the most intensively researched of all the Drepanidinae (Banko *et al.* 2002a), and insight from this species can be used to guide research and management for other endangered members of this subfamily. Honeycreepers with similarly long lifespans and extended parental care periods, such as the Maui parrotbill (*Pseudonestro xanthophrys*; Simon *et al.* 1997) and ʽakiapōlāʽau (*Hemignathus munroi*; Pratt *et al.* 2001), could also display a delay in male breeding, elevated female mortality, and a biased sex ratio. Both species are highly endangered and their breeding ecology make the collecting of sufficient data for a study such as ours impractical, so our results could be used as a proxy or guide for future researchers, modelers, and managers.

Our results also confirm the difficulty of sexing subadult age classes. The majority of SY individuals were classified as females, while ASY individuals were predominantly males; leading to an operational sex ratio of near unity for the PCR combined with the plumage sample. The preponderance of ASY males and their presumed advantage in attracting mates, serve as a proximate explanation for the delayed breeding in SY males in palila (Rohwer *et al.* 1980, Studd and Robertson 1985). However, more research is required to fully understand the suite of factors influencing the mating system (e.g., absence of polyandry, possible age-based variation in testosterone levels).

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7 DISEASE

Paul C. Banko, Carter T. Atkinson, Susan I. Jarvi, Luanne Johnson

Introduction

The palila (*Loxioides bailleui*) occurs above the range of mosquitoes that transmit avian malaria and pox, and there is little indication that palila are frequently exposed to these diseases (Banko *et al.* 2002). Nevertheless, palila are sensitive to malaria (van Riper *et al*. 1982). Malaria, pox, and other diseases may have contributed to their extirpation from lower elevations where they ranged historically (Banko *et al.* 2009). Therefore, habitats where mosquitoes occur may prevent the successful reintroduction of palila due to their exposure to diseases.

Although there are few disease concerns in habitats currently occupied by palila, it is important to determine the incidence of mortality that might be attributable to disease. For example, some palila embryos die before completing development, or they complete development but do not hatch. Others hatch and develop normally but die about halfway through the nestling stage (see Chapter 9: Breeding Phenology, Productivity, and Nesting Success; U.S. Geological Survey unpublished data).

Ten chicks died in 1996 at Keauhou Bird Conservation Center soon after hatching from eggs collected from wild nests, and infection from *Mycoplasma* bacteria was initially reported (B. Rideout, San Diego Zoo Institute for Conservation Research [SDZICR], personal communication). In a limited sample of wild adult birds tested in the fall of 1996, evidence of *Mycoplasma* was discovered in 2 of 11 palila and 2 of 10 Hawai‘i ‘amakihi (*Hemignathus virens*; T. Work, U.S. Geological Survey, personal communication). These results suggested that *Mycoplasma* might contribute to the mortality of wild palila chicks. Therefore, we investigated the occurrence of mosquitoes and the prevalence of malaria and *Mycoplasma* in palila and other bird species on Mauna Kea.

Methods

Mosquito Monitoring

We stationed three oviposition traps baited with organically rich "stinky water" along an elevation gradient within the North and South sites (see Introduction for site locations). The traps were run continuously for about two weeks during September 1996 when the probability of trapping mosquitoes was relatively high.

Avian Malaria and Pox Screening

During October 1996, we captured 11 palila in mist-nets at PL Mauka on the western slope of Mauna Kea and collected blood and culture samples for disease screening. With T. Work and G. Massey (Hawai‘i Division of Forestry and Wildlife), we collected blood smears and plasma for malaria screening by microscopy and serology (Atkinson *et al.* 2001) and cloacal and choanal swabs for viral and bacteriological assays. Virology assays were conducted at the National Wildlife Health Laboratory in Madison, Wisconsin, and bacteriology assays were performed at Texas Veterinary Medical Diagnostic Laboratory in College Station, Texas.

Mycoplasma Screening

To determine the prevalence of *Mycoplasma* bacteria in the wild palila population, we used sterile applicators to swab the choana (opening of nasal cavity into the mouth) of adult birds captured in mist-nets within palila habitat in 1998 and 1999. We also took a sample of the albumin from wild palila eggs that did not hatch. In 1998, swabs were placed in a growth medium of 3 ml Frey's media (Frey's medium with 10% swine serum, cysteine hydrochloride, and NAD) containing 10% thallium to prevent overgrowth by other bacteria. The cultures were stored at room temperature until their transfer to Kīlauea Field Station (U.S. Geological Survey), in Hawai'i Volcanoes National Park, where they were incubated at 37°C for 4–5 days, then passaged into media without thallium. Cultures were passaged an additional two times at 4–5 day intervals. At the end of the last passage, cultures were plated onto Frey's agar and incubated for 4–5 days. If a colony of bacteria consistent with *Mycoplasma* grew on the agar plate, it was sent to a laboratory in North Carolina for identification to species level.

We also used PCR (polymerase chain reaction) methods to attempt to isolate DNA from *Mycoplasma* bacteria in wild palila in 1999. After swabbing the choana of a palila, we cut the applicator tip off and dropped it directly into approximately 500 µl DNA lysis buffer (0.1M ris- Cl pH 8.0, 0.1 M sodium EDTA, 2% SDS). Egg tissue from unhatched embryos was collected and a small sample placed in DNA lysis buffer. All samples were transferred to Kīlauea Field Station and were frozen until extraction. DNA was extracted from tissue samples (DNeasy Tissue Kit®, Qiagen) and eluted into 400 µl buffer AE (according to manufacturer's protocol). DNA was quantified by spectrophotometry (Spectronic Instruments).

The PCR primers F1 and R1 (Lauerman *et al*. 1995), specific for 16S through the spacer region to 23S RNA genes, were synthesized (BMBITF/PBRC, University of Hawai'i at Mānoa, Honolulu, HI; June 1999). The PCR reactions were set up in 25 µl volumes as described by Lauerman *et al*. (1995) with some modification. Cycling conditions were 94°C for 30 seconds, 54°C for 2 minutes, and 72°C for 2 minutes, for 40 cycles. Cultured samples from zebra doves (*Geopelia striata*) and rock doves (*Columbia livia*) served as positive controls in all PCR reactions. The PCR products were analyzed by electrophoresis in 1.5% agarose (Nusieve FMC 3:1 agarose) gels stained with ethidium bromide. For cloning, PCR products of the size of interest (approximately 400–1000 bp) were gel isolated (Qiagen® gel extraction kit) and ligated into pCR™II vector (TA Cloning® kit, Invitrogen) following the manufacturer's protocols. Alternatively, some PCR products were gel isolated and subjected to direct sequencing. Sequencing was completed on clones on both strands (ABI 373 cycle sequencing, BMBITF/PBRC, University of Hawai'i at Mānoa, Honolulu, HI).

Results

Mosquito Monitoring

No mosquitoes were trapped or otherwise detected in the North or South sites (Figure I.1). Mosquitoes were not detected in any of the study sites occupied by palila. At Kīpuka 'Alalā, mosquitoes were detected in association with a sewage pit. Mosquitoes were possibly detected by staff in PFlats, but only incidentally.

Avian Malaria and Pox Screening

All 11 palila sampled tested negative for malaria, and none had pox lesions. Choanal swabs from 2 of 11 palila were determined by PCR assay to be positive for *Mycoplasma* bacteria, but all cultured samples were negative and strains of the bacteria could not be identified. Virology results were negative for three palila sampled (T. Work personal communication).

Mycoplasma Screening

No palila were swabbed for *Mycoplasma* in 1997; however we cultured swab samples from 43 palila, 8 palila eggs, 14 'apapane (*Himatione sanguinea*), 13 'i'iwi (*Vestiaria coccinea*), 19 Hawaiian ʻamakihi, 7 house finch (*Carpodacus mexicanus*), 4 Japanese white-eye (*Zosterops japonicus*), 3 red-billed leiothrix (*Leiothrix lutea*), 2 yellow-fronted canary (*Serinus mozamibicus*), 2 zebra dove, 1 ʻelepaio (*Chasiempis sandwichensis*), and 1 Eurasian skylark (*Alauda arvensis*) between August 1998–July 1999 in palila habitat. Only one zebra dove cultured positive for *Mycoplasma* bacteria.

Approximately 80 samples were extracted from swabs for PCR analysis. The PCR results were obtained from 62 samples. A total of 9/62 (14.5%) samples tested produced multiple bands. The positive dove controls were clearly positive, producing a single distinct band of approximately 600 bp in all tests. The bands from the two dove species cultures were cloned and sequenced. Both appear to be *Mycoplasma* sequences, based on a GenBank® (National Center for Biotechnology Information, Bethesda, MD) search. The cloned sequence from the zebra dove culture matched closest with a *Mycoplasma* sequence from a turkey (*Meleagris gallopavo*); while the sequence from the rock dove culture matched closest with several human *Mycoplasma* spp.

Several samples from palila eggs produced multiple clear bands, some of which were in the 400–700 bp range. Two of these bands were directly sequenced from an unhatched egg from 1999. One of these bands appeared to be a *Mycoplasma* sequence based on a GenBank search. Although the sequence did not match clearly with any known sequences in GenBank, its closest match was with human *Mycoplasma* spp. Later, we learned that another research group had cultured *Mycoplasma* from a captive palila hatched from a wild egg three years earlier. After obtaining the partial 16S-23S RNA genes, PCR amplification reactions were carried out under various conditions for optimization of the primers. An annealing temperature of 55°C was selected, and a total of 14 products were cloned from five individuals using these primers as described above.

Discussion

Mosquito Monitoring and Avian Malaria and Pox Screening

Avian malaria is unlikely to affect the existing palila population or future reintroduced populations in subalpine Mauna Kea, where mosquitoes and other vectors are absent or rare (Banko *et al.* 2009). In addition, lesions caused by avian pox virus are rarely observed in palila; although lesions occur more frequently in bird species that seasonally leave the lower-elevation, wetter forests of windward Mauna Kea to feed on māmane flowers within the palila's range (Hess *et al.* 2001, U.S. Geological Survey unpublished data). Despite proximity to pox- and malaria-infected birds, the lack of an effective vector protects the palila. Nevertheless, additional screening for avian diseases and vectors is warranted within Pōhakuloa Training Area sites (see Figure I.1) because of their lower elevation.

Mycoplasma Screening

The effects of bacterial diseases and other pathogens are of concern to palila management because of their possible implication in the deaths of captive chicks. Although *Mycoplasma* bacteria have been cultured from a zebra dove, they were not cultured from wild palila or other honeycreepers captured in palila habitat on Mauna Kea.

During a meeting of the Hawaiʻi Forest Bird Recovery Team (16 November 2000), U.S. Fish and Wildlife Service officials and representatives of the SDZICR concluded that *Mycoplasma* was not implicated in the 1996 mortality of captive palila chicks. Rather, *Pseudomonas aeruginosa* probably killed the chicks and routine avicultural precautions would be expected to prevent a reoccurrence (B. Rideout and P. Morris, SDZICR, personal communication). Although *P. aeruginosa* had been suspected of killing the chicks in 1996 (T. Work and G. Massey personal communication), SDZICR veterinarians suggested at that time that *Mycoplasma* was the more likely agent (B. Rideout personal communication). Following this decision in 2000 and believing that *Mycoplasma* was not a threat to palila, we decided to abandon our efforts to isolate *Mycoplasma* in palila and other bird populations on Mauna Kea.

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8 BREEDING DEMOGRAPHY

Paul C. Banko, Chris Farmer, Luanne Johnson, Colleen Cole

Introduction

The behavior of individually identifiable palila (*Loxioides bailleui*) at their nests can provide valuable insights into the characteristics and reproductive trends of the breeding population that may not be possible otherwise. Young and adult palila banded since 1987 by U.S. Geological Survey staff composed a substantial pool of marked individuals for breeding studies. We banded additional birds to investigate aspects of palila breeding demography, including dispersal from natal nests, changes in nest-site selection, age distribution and longevity, as well as mate selection and fidelity among breeding seasons.

Another goal of our study was to identify relationships between male helpers at nests (Pratt *et al.* 1997, Miller 1998) and the nesting pair. The sex ratio of adult palila is biased towards males (Lindsey *et al*. 1995; see Chapter 6: Sex Ratio); thus, the availability of females may constrain the productivity of the population in some years and prompt some unmated males to help at nests or some females to mate with several males. Helpers may enhance their chances for acquiring a mate or nesting experience when nesting opportunities are limited due to a shortage of mates or favorable nesting sites.

Understanding variation in breeding behavior may help develop recovery strategies for endangered species because the dynamics of small populations could be disproportionately affected by individuals or pairs having greater experience or a particularly favorable suite of behaviors. Identifying how often and under what environmental conditions individuals breed may help explain some of the substantial variation in the total breeding effort in the palila population over time (see Chapter 9: Breeding Phenology, Productivity, and Nesting Success). Studying the breeding behavior of the palila is especially important because their reproductive capacity is relatively low and the population has been declining rapidly (see Chapter 5: Population Trends and Response to Environmental Factors).

Methods

We searched for palila nests in every tree within a 50-m-wide strip along transects that were 900–7,500 m long on the western slope (see Figure 9.1, Chapter 9: Breeding Phenology, Productivity, and Nesting Success), during 1999−2003. We attempted to identify all nesting adults using either of two methods: recording color band combinations of previously banded adults, or capturing and banding birds, including individuals that had lost one or more of their original color bands. The pool of banded birds allowed us to assess nesting histories, age distributions, longevity, nest site selection, and individual dispersal from natal nests.

We set mist-nets around nest trees to capture the adults when chicks in the nest were ≥4 days old. We used plumage characteristics to determine age categories using Jeffrey *et al*. (1993): after-second-year (ASY), second-year (SY), or hatch-year (HY). Recaptured birds were exactly aged when possible, based upon their age at first capture. Any HY birds caught at a nest and subsequently observed begging for food from the nesting adults were assumed to be from a previous nest within the same breeding season. All palila were weighed, measured, and banded with a unique sequence of three color bands and a numbered aluminum band.

We calculated capture rates using adults identified by observations in the field (re-sighting) or by capture of nesting adults. In order to avoid capture-rate bias, we only included active nests where mist-netting was attempted or previously banded birds could be more readily observed. Secondary males helping at nests were included as nesting adults in our capture rate analysis. Using the UTM (Universal Transverse Mercator) coordinates of each nest, we measured the distance between successive nest attempts within and between breeding seasons. When nesting adults had been banded in a previous season as nestlings, we calculated dispersal distance (meters) between their adult and natal nests using the measure tool in ArcView GIS 3.2 (ESRI 1999). After training from Greg Massey (DVM, Division of Forestry and Wildlife, state of Hawai'i), we collected blood (brachial or leg vein) or pin (blood) feather samples from nesting adults, nest helpers, and chicks during 1999−2002 to acquire DNA for assessing paternity of embryos and chicks. We collected DNA from 25 complete families and 6 incomplete families during 1999–2000. Nest helpers were sampled from 7 of these 31 families, including 4 in 1999 and 3 in 2000. We banded and collected blood from chicks when they were 14 days old. Blood and pin feathers were collected in heparinized hematocrit tubes, promptly expressed into tubes containing lysis buffer, stored in coolers, and transported to Kīlauea Field Station (U.S. Geological Survey). Susan Jarvi (University of Hawai'i at Hilo) extracted DNA for sex and paternity identification.

Results

The number of active palila nests found along the survey transects on the western slope of Mauna Kea ranged between 11–37 during 1999–2002, but none were discovered in 2003 (see Chapter 9: Breeding Phenology, Productivity, and Nesting Success). We identified previously banded nesting adults (recaptures) and banded many newly captured adults at some of these active nests (hereafter, "marked nests"). We could not identify every nesting adult at marked nests due to difficulties in mist-netting or observation. We identified or caught between 74–100% of adults at marked nests each season (Table 8.1). The proportion of nesting adults that were recaptured ranged between 57–90%, while the proportion of newly captured nesting adults ranged between 10–43%.

Table 8.1. Marked nests (nests attended by banded adults) and identification or capture status of nesting adult palila (including potential nest helpers) on the western slope of Mauna Kea, Hawai'i, 1999–2003. No nests were found in 2003.

	1999[1]	2000[2]	2001	2002
Active nests	37	36	11	25
Marked nests	24	28	5	17
Adults banded (%)	42 (82)	52 (88)	10 (100)	25 (74)
Adults newly captured	18	21	1	5
Adults recaptured	24	31	9	20

[1] Three nests in 1999 had an extra male that helped at the nest (*n* = 3 helpers).

[2] Three nests in 2000 had an extra male that helped at the nest (*n* = 3 helpers).

We identified 49 females and 48 males from pairs that nested at least once during 1999–2002 (Table 8.2). Forty females were observed nesting in only one of the four years, primarily 1999 or 2000. Relatively few marked females nested in 2001. Four females nested twice in a single season, and one re-nesting attempt was observed in each of the four years. Eight females

Table 8.2. Distribution of nesting effort among a marked sample of palila on the western slope of Mauna Kea, Hawaiʻi, 1999–2002. Marked sample includes 49 females and 48 males.

	Total	1999	2000	2001	2002
Females nesting		20	23	4	11
Males nesting		18	25	4	12
Females nesting twice per season		1	1	1	1
Females nesting in 1 of 4 years	40	15	15	2	8

nested in two years, and one female produced three nests, one in 2000 and two in 2001. Annual breeding attempts were similar for males, but three males nested three times: one nested in three different years and the other two males nested once in one year and twice in another year.

Of 278 palila chicks that were banded in their nests during 1987–1998, we identified six (three females, three males) as breeding adults during 1999–2002. A 1991 male nestling nested on three occasions during 1999–2002; a 1996 male nestling nested in 2002; and a 1998 male nestling nested in 2000. Two females that were banded as nestlings in 1998 also nested in 2000, and a 2000 nestling female nested in 2002.

We knew the exact ages of up to 33% of the nesting palila each season during 1999–2002 (Table 8.3). We could not exactly age any bird in 2001 because all observed birds were originally banded as ASY. We calculated the mean age of breeders during 1999–2002 using our exact age determinations. The mean breeding age varied annually between 4.2–6.1 years, with an overall range of 2–13 years (Table 8.3). The proportion of nesting adults older than 6 years ranged between 14–19% each year.

Table 8.3. Number of known-age, nesting palila, with mean age and number of breeders ≥6 years, on the western slope of Mauna Kea, Hawaiʻi, 1999–2002.

	1999	2000	2001	2002
Known-age nesting palila/all known-age adult palila[1] (%)	8/39 (21)	15/52 (29)	0	7/21 (33)
Range of ages (years)	2–8	2–11	—	2–13
Mean age (years ± SE)	4.8 ± 0.96	4.2 ± 0.68	—	6.1 ± 1.62
Nesting palila ≥6 years old (%)	7 (18)	10 (19)	0	3 (14)

[1] The number of known-aged palila is less than total adults identified (Table 8.1) because of uncertainties in aging birds when they were first captured.

During 1999–2002, the oldest breeding palila we detected was ≥13 years of age. Three 10-year-old birds (two females, one male) were associated with fertile clutches in 1999. Three 11-year-old birds (two females, one male) were associated with fertile clutches in 2000; the male nested with a two-year-old female. Also in 2000, a ≥13-year-old male was the principal male or helper at a nest that produced infertile eggs, the other affiliated male was at least four years of age, and the female from that unsuccessful nest was two years old. In 2001, one nesting adult was at least eight years old and was associated with one of only two successful nests of the season. In 2002, one male and one female (nesting pair) were at least seven years old. Additionally, a 13-year-old male and an 11-year-old female were each associated with fertile clutches in 2002.

There was a marginally significant difference in the age distribution of nesting palila and palila that were captured at long-term banding stations and were not known to be nesting (non-breeders) during 1999–2002 (χ^2 = 13.55, P = 0.06). This difference was due to the greater representation of nesting birds in the 9–10 year age class compared to the non-nesting population (Figure 8.1).

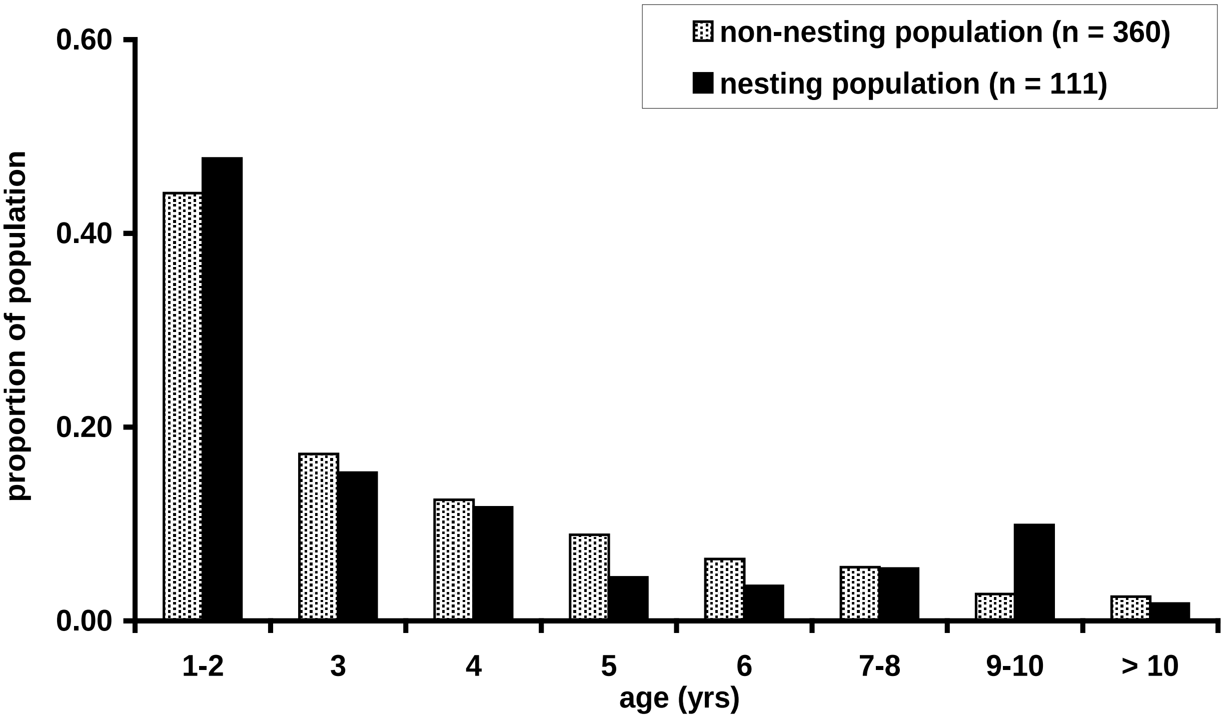

Figure 8.1. Age distribution of nesting palila and non-nesting palila (birds that were not associated with nests) on the western slope of Mauna Kea, Hawai‘i, 1999–2002.

The mean distance from natal nests (where a banded individual was fledged) to adult nests (where the same individual tended a nest as an adult) during 1999–2002 was 618 ± 69.4 m (± SE; range = 339–889; n = 8; three males, three females in 2000; one male, one female in 2002; Table 8.4). The mean distance between natal and adult nests was similar for males and females. Of this sample, two females and one male were banded as nestlings in 1998, and they first bred in 2000. A nine-year-old male nested over 2000 m from his natal nest in 1999, but only 400 m from his natal nest in 2000. A four-year-old male nested approximately 300 m from his natal nest in both 1999 and 2000. In 2002, a six-year-old male nested ≥500 m from his natal nest, pairing with a two-year-old female that had dispersed 800 m from her natal nest.

Table 8.4. Distances between the nests of individual palila on the western slope of Mauna Kea, Hawai'i, 1999–2002. Natal nests are the nests from which marked individuals fledged, and adult nests are the nests they tended as adults.

	Mean distance (m)	Distance range (m)	Number of palila	Number of nesting pairs or individuals
Natal and adult nests, 1999–2002	618 ± 69.4	339–889	8	1 banded pair 6 individuals
Successive adult nests within the same season, 1996–2002	155 ± 31.5	26–419	11	4 banded pairs 7 individuals
Adult nests between seasons, 1999 & 2002	370 ± 90.5	55–1723	24	
Adult nests between seasons, 1999 & 2000	389 ± 268.3	55–1723	6	3 banded pairs 3 individuals
Adult nests between seasons, 2000 & 2001	189 ± 97.4	91–286	2	1 banded pair, 2 nests within season
Adult nests between seasons, 2001 & 2002	43 ± 126.3	138–1389	12	8 individuals

The average distance between successive nests within the same year ranged between 43–389 m during 1999–2002.

We collected DNA from 25 complete families and 6 incomplete families during 1999–2000. Nest helpers were sampled at 7 of these 31 families, including 4 in 1999 and 3 in 2000. Relatedness tests based on exclusion and similarity coefficients (Bionumerics v. 2.0) suggested that the helper males were more related to the offspring in the nests they attended than to randomly sampled adults in the population (Patch-Highfill 2008).

Discussion

We identified >87% of the adults at active nests during 1999–2002, but conclusions about the frequency of breeding of individuals are limited because few pairs apparently nested in 2001 and no nests were found in 2003. Most individuals were observed breeding in only one year, but this may have been partly due to the difficulty in finding all nest attempts during breeding seasons that extended for months and along transects that were only 50-m wide. Thus, we were unable to determine whether the low frequency of nesting observed in successive years was due to frequent changes in nesting sites or low survival.

Relatively few birds that were banded as nestlings before 1999 were identified as breeding adults during 1999–2002, and most were only several years of age when they nested. Lindsey *et al*. (1995) estimated mean (± SE) annual survival of after-hatch-year birds as 0.63 ± 0.05. Therefore, it was unexpected that almost 20% of nesting adults that could be identified in 1999, 2000, and 2002 were older than six years or that a few adults older than ten years were breeding each year. Breeding palila were significantly older than birds not associated with nests, due mainly to a greater proportion of 9–10-year-old birds in the breeding population. We did not determine whether older or more experienced parents had higher fledgling success rates, but we suspect that experienced adults formed a larger proportion of the breeding population in years when food availability was marginal (1999, 2000, 2002) than when it was abundant (1996; see Chapter 16: Māmane Phenology).

Our mean within-season distance between nests of the same individual (155 m) was similar to the 141 m obtained by Pratt *et al.* (1997), but the mean distance between nest locations in different years of the same individuals was 370 m compared to 127 m. Moreover, our range of 55–1722 m (*n* = 24 birds) indicated considerable annual variability in the nesting location of individuals. The distance between nests among years was not significantly different for males or females. We presume that nest location was influenced mainly by the seasonal distribution of food, patchiness of the habitat, or prior nest success, but our limited data did not allow us to test these hypotheses.

From year-to-year, the nest attempts of some palila were separated by >1.7 km. Although Fancy *et al.* (1993) documented limited dispersal by palila, our results suggest that palila should readily colonize restored habitat adjacent to or near their core range.

The results of genetic studies indicate that males may gain nesting experience by helping at the nests of parents or close relatives (Patch-Highfill 2008), which likely increases nesting success and reduces the overall costs of nesting (Miller 1998). Nest helping by males may increase if the sex ratio becomes increasingly male-biased.

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9 BREEDING PHENOLOGY, PRODUCTIVITY, AND NESTING SUCCESS

Paul C. Banko, Chris Farmer, Luanne Johnson, Steven C. Hess, Colleen Cole, Steve J. Dougill, Kevin W. Brinck

Introduction

Sustained, successful nesting by palila (*Loxioides bailleui*) is required for the species' recovery, yet palila reproduce at a relatively low rate and are likely to respond slowly to habitat restoration (Banko *et al.* 2002b, Banko *et al.* 2009). For example, palila usually lay only two eggs per clutch, and few pairs produce more than two fledglings per year (Pletschet and Kelly 1990, Pratt *et al*. 1997, Banko *et al.* 2002b). Drought, predators, and other demographic and environmental factors may also limit palila productivity (Lindsey *et al*. 1995, Lindsey *et al*. 1997, Banko *et al.* 2013).

The initiation and duration of the breeding season varies considerably each year and affects the production of offspring (Banko *et al.* 2002b). Food availability explains much of this annual variation (Pratt *et al*. 1997, Banko *et al.* 2009), but because māmane provides most of the palila's food, reproductive success might also differ between the two major forest types on the western slope of Mauna Kea: māmane (*Sophora chrysophylla*) and mixed māmane-naio (*Myoporum sandwicense*). Because māmane trees are more abundant in māmane-dominant forest, generally occurring at higher elevations compared to mixed forest (Hess *et al.* 1999), factors affecting reproduction may not be uniformly distributed across the landscape.

Palila productivity should be affected by the number of pairs attempting to nest each year, number of nests attempted by each pair during each season, clutch size, fertility and hatchability of eggs, and growth and survival of chicks. We investigated these and other factors in order to understand intrinsic and environmental constraints on productivity.

Methods

Nesting Phenology

We studied palila breeding ecology from 1996 to 2004. In teams of three to five, we searched for palila nests in every tree within a 50-m-wide strip along transects that were 900–7500 m long. Palila study grid (PSG) transects were located in the Mauka, Makai, Manao, and Ahumoa study grids on the western slope of Mauna Kea (Figure 9.1). Mauka and Makai grids included 24 transects in māmane-dominated forest. Manao and Ahumoa grids included 10 transects in naio-dominant forest. The eight Hawai'i Forest Bird Survey (HFBS) transects on the western slope began above the upper grid (Mauka) and extended below the lowest grid (Ahumoa). They passed through both māmane and naio-dominant forest.

We grouped the nests into three categories (Table 9.1): active nests, inactive nests, and supplemental-fed nests. Active nests were attended by adults. Inactive nests were not attended but looked as if they had been attended earlier in the season because the nest materials looked relatively fresh; the nest cup was not full of leaves or other debris (e.g., spider webs); the lichen in the nest lining was compact (not becoming overgrown); the body of the nest was not misshapen or partially disintegrated, and feces had accumulated on the nest rim (at nests where chicks had apparently survived more than about 10 days). We had little difficulty distinguishing between inactive nests of the current season and those of previous years because we saw how active nests aged in appearance as we encountered them during the course of the season. Finally, supplemental-fed nests were active nests in which we augmented

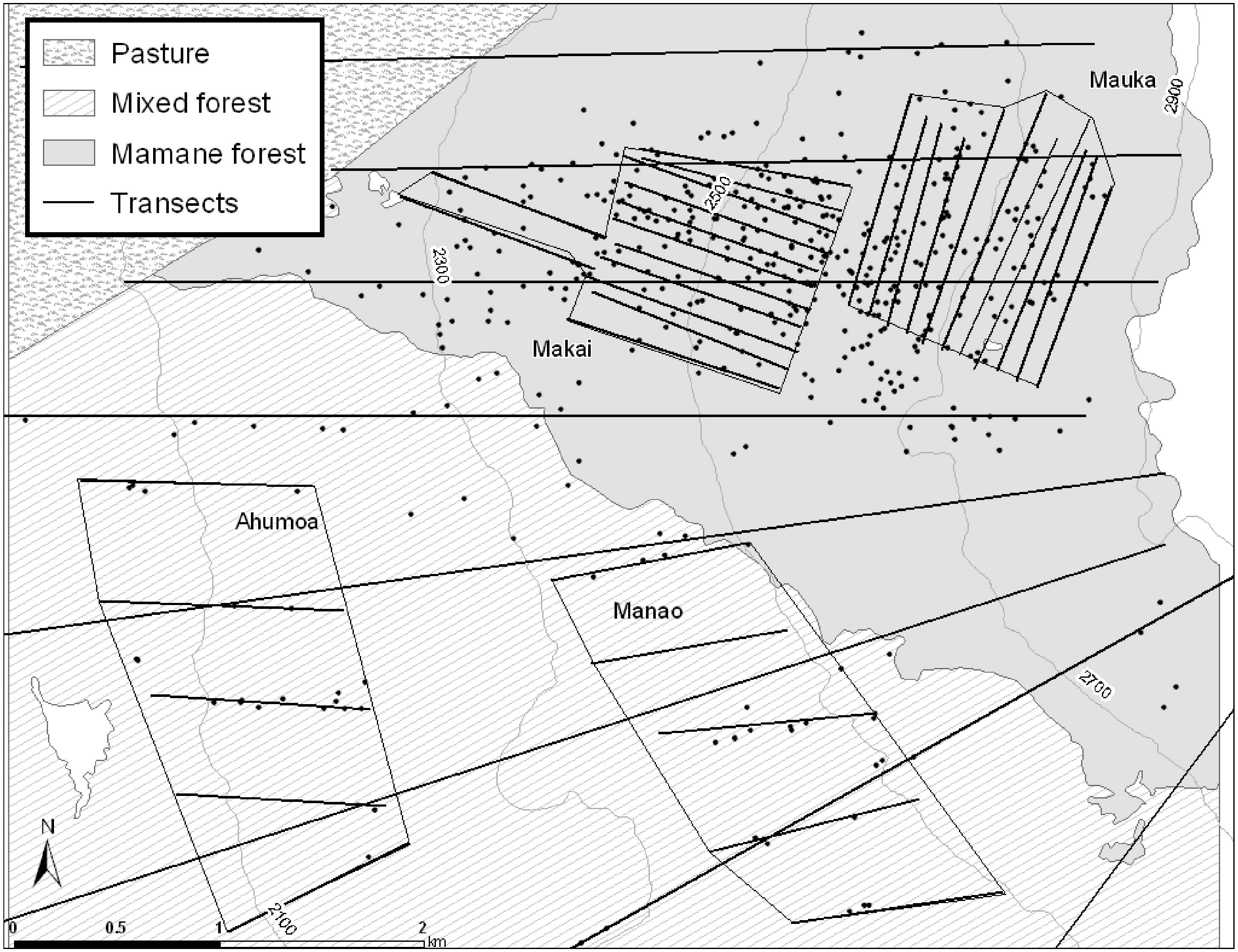

Figure 9.1. Palila study grids and nest locations (dots) on the western slope of Mauna Kea, Hawai‘i, 1996–2004.

Table 9.1. Palila nests found on the western slope of Mauna Kea, Hawaiʻi, 1996–2004.

Year	Total nests	Active nests (monitored)	Inactive nests	Supplemental-fed nests
1996	153	63 (46)	86	4
1997	57	12 (12)	45	0
1998	49	21 (21)	28	0
1999	69	37 (37)	32	0
2000	70	36 (36)	32	2
2001	17	11 (11)	6	0
2002	40	25 (25)	15	0
2003	5	0 (0)	5	0
2004	15	7 (7)	8	0

the diet of the chicks, but for this reason we did not include them in the analyses of productivity (see Chapter 3: Harvesting Wild Eggs and Supplementing Food at Nests).

Nest searching effort before, during, and after the peak breeding season (April–August) varied from year to year (Table 9.2). Even though active palila nests have been found from January through October (Pratt *et al*. 1997, Banko *et al.* 2002b), the majority of our search effort was spent during the peak breeding season. We did not search for nests before the peak breeding season in 1997, 1998, 2003, and 2004. We visited certain areas multiple times during the breeding season to detect nests initiated at different times and focused on transects in the māmane-dominated forest (i.e., the Mauka and Makai study grids). During 1999−2004, we also searched for nests opportunistically (not systematically along transects) in apparently suitable habitat. In 2004, we found palila nests by tracking radio-tagged females. Data from nests discovered opportunistically and by radio tracking was not included in analyses sensitive to annual variation in search effort or nesting density. We determined the overall length of the nesting season by back-calculating the number of days between the first-laid egg and the last active nest using the nesting phenology in Banko *et al.* (2002b).

The area searched for nests was 25 m on each side of a transect. We calculated the overall search area by multiplying the width, 50 m, by the length of the transect searched. Overall nest density was calculated from the number of nests found within the area searched along each PSG or HFBS transect (Table 9.3).

We searched for nests during 1989–2004, but we analyzed only the results generated from standardized surveys (1996–2004) to calculate the number of nests per unit area in each study grid. We fit a general linear model to predict the number of nests detected per hectare as a function of māmane phenology (see Chapter 16: Food Availability: Māmane Phenology) in the four study grids where nest surveys were conducted. Using ln (nests/100 ha + 0.5) as the response parameter, the mean monthly number of flowers and pods per tree on the western slope during September–April (the months before the breeding season) were tested as predictors of nests found per area searched.

Nesting Production and Recruitment

We marked the location of all active nests and returned within a few days to determine whether the female was incubating eggs or brooding chicks. We observed the nest from a distance of

Table 9.2. Area (ha) searched for palila nests before, during, and after the main breeding season (April–August) on the western slope of Mauna Kea, Hawaiʻi, 1996–2004. Palila study grid (PSG) and Hawaiʻi Forest Bird Survey (HFBS) transects are included.

	PSG transects: Mauka, Makai (māmane-dominant forest)			PSG transects: Manao, Ahumoa (naio-dominant forests)			HFBS transects		
Year	Before breeding	During breeding	After breeding	Before breeding	During breeding	After breeding	Before breeding	During breeding	After breeding
1996	5	715.9	135.6	0	36.8	0	0	0	0
1997	0	110.9	132.1	0	0	42	0	24.8	178.5
1998	0	278.1	95.8	0	36.8	15.8	0	65.3	192.8
1999	48	344.4	85.1	3	47.3	47.3	0	217.5	105
2000	21	138.1	79.1	0	15.8	47.3	5	99.8	63
2001	24	275.4	0	8	36.8	10.5	29	195	36
2002	23	163.8	0	0	31.5	22.5	0	141	78
2003	0	113.4	18.9	0	10.5	5.3	0	66	20.3
2004	0	0	71.4	0	0	31.5	0	0	116.3

Table 9.3. Nest density (nests per ha searched) for active and inactive palila nests in māmane-dominant and naio-dominant forests on the western slope of Mauna Kea, Hawaiʻi, 1996–2004. Density is given by Palila study grid (PSG) and Hawaiʻi Forest Bird Survey (HFBS) transects.

	Māmane-dominant forest			Naio-dominant forest		
Year	PSG	HFBS	PSG & HFBS	PSG	HFBS	PSG & HFBS
1996	0.54	N/A	0.54	0.27	N/A	0.27
1997	0.12	0.11	0.12	0.12	0.07	0.09
1998	0.12	0.07	0.10	0.06	0.03	0.04
1999	0.15	0.08	0.12	0.06	0.04	0.05
2000	0.18	0.03	0.12	0	0	0
2001	0.05	0	0.03	0	0.01	0.01
2002	0.07	0.06	0.07	0.02	0.05	0.01
2003	0.01	0	0.01	0	0.08	0.04
2004	0.08	0.03	0.06	0.13	0	0.05

≥15 m while concealed within a blind or behind vegetation. When the female was absent from the nest, or if no activity was observed for at least 30 minutes, we examined the inside of the nest using a mirror mounted on an extendable pole. We attempted to determine the status of eggs or chicks twice each week in 1996, and once every week in 1997 and 1998. In 1999, we visited active nests daily. During 2000–2002 we visited nests every day during the week, excluding weekends. In 2004, we checked nests every other day and more often if necessary. Although the schedule for checking nests varied, the fact that nests were checked at least weekly provided adequate resolution for our analyses. We determined the month of nest initiation for all active nests by subtracting 17 days from the hatch date of the chicks. This included 16 days of incubation and an extra day for laying the first egg (Banko *et al*. 2002b). We assumed that incubation began on the day the second egg was laid.

We banded chicks at 10–15 days of age during 1996−1998. During 1999–2004, we banded chicks of known age on day 14 (day 15 in a few cases) if they were large enough; we banded chicks of unknown age when they were estimated to be 10–16 days of age. We used a general linear model in S-Plus (version 6) to examine the between-year differences in the weight of chicks that were 10–16 days old with age (in days), tail length (mm), and hatch year as covariates.

We determined fertility, hatchability, and fledging rates using data from active nests in which the fate of the entire clutch was known. We used a χ^2 test to determine if the proportion of successful nests varied between years. We determined fertility on the basis of whether eggs hatched or contained at least rudimentary blood vessels when opened within 1–5 days after the nest was abandoned. We did not determine fertility when the egg contents were not sufficiently fresh to examine accurately, and these results were excluded from estimates of fertility. We also determined the fertility of three eggs from two nests found opportunistically on the northern slope of Mauna Kea.

Causes of Nest Failure

We monitored a subset of active nests (incubation stage) with video cameras during the 1998–2002 breeding seasons to determine the causes of nest failure (see Chapter 11: Behavior at Nests). Beginning near the ground under the nest tree, we gradually moved a camera up towards each nest in 1-m increments while the adults were absent. From a blind, we observed the behavior of the adults when they returned to evaluate whether the cameras affected their behavior. If either adult behaved unusually or seemed distressed, we moved the cameras back to the last position and postponed further efforts to move cameras closer to the nest for one day. On the following day, we moved the camera towards the nest in <1-m increments. Eventually, we placed the cameras within 15–30 cm of the nest to record activity. We placed videocassette recorders and power sources 30 m from the nest tree. In 1998 and 2000, we changed videocassettes every 24 hours, except on weekends when staff was not in the field. In 1999, 2001, and 2002, we changed videocassettes every day. The change in surveillance from five to seven days per week would not likely have affected the interpretation of results significantly because gaps in surveillance occurred at other times due to technical difficulties and because we monitored nests at least weekly by direct inspection regardless of whether or not it was being monitored with video.

Video surveillance continued until chicks fledged, the nest failed, or the camera system failed. We monitored nests without cameras until chicks fledged or the nest failed. Furthermore, we investigated the cause of failure by thoroughly and systematically inspecting the nest, nest tree, and the surrounding area including the ground below the nest. We also recorded detailed nest observations to provide more information in determining nest fate.

Results

Nesting Phenology

The mean length of the nesting season was 125 ± 21.3 days (± SE; range = 53–205 days) in 1996–2002. In 2003, none of the nests we found were active, and in 2004 we started our nesting survey late in the season. Therefore, we could not determine the length of the breeding season in these two years. We found the fewest nest attempts in 2003 among all nine years. In 1996, active nests were found in eight months (20 February–13 September), the longest nesting period during the study. Nest initiation peaked in May during 1996, 1997, 1999, and 2002, but in 1998 nesting peaked in June (Figure 9.2). In 2000, the nesting season ended abruptly, peaking first in May and then again in July but with no new nests afterward. Nests were initiated at a relatively steady rate during May–July 2001. In 2002, palila began breeding earlier and continued later than they had since 1996, possibly resulting in multiple nesting attempts by at least some pairs. Māmane pods were abundant earlier in the 2002 breeding season than they had been in 2000 or 2001 (see Chapter 16: Food Availability: Māmane Phenology). Despite the early and abundant pod crop, we found fewer nests in 2002 than we did in 1999 or 2000. During 1996–2002, we found the majority of nests in māmane-dominated PSG and HFBS transects. In 2003, on the other hand, nest density was higher in the naio-dominant forest, and in 2004, nest density was similar in both types of forest (Table 9.3).

Our general linear model revealed that the mean number of flowers in September, April, March, and January significantly predicted the number of nests, when 2004 was excluded (Table 9.4). No predictors were significant when 2004 was included in the model, suggesting the alternative hypothesis that 2004 was qualitatively different from previous years.

When we compared the predicted number of nests found to the actual results from our 2004 nest searching, the predictions were lower than the actual outcome (Table 9.5). In addition to the predictive model based on flowers, we explored possible explanatory models using data collected during and after the breeding season. We found a positive exponential relationship ($r^2 = 0.59$, $P = 0.01$) between the mean number of pods per tree with the active nest density within the same breeding season (Figure 9.3).

Nesting Production and Recruitment

We deduced from nesting studies that fecal deposits on the rims of inactive nests were a reliable indication that chicks survived ≥10 days after hatching. The absence of fecal deposits indicated that no eggs were laid, eggs did not hatch, or chicks died and disappeared from nests <10 days after hatching. During 1996–2004, we found some inactive nests with abandoned or broken eggs or dead chicks (Table 9.6), but at least one chick fledged from 108 (55%) of the 195 active nests we monitored (Table 9.7). An average of 1.5 ± 0.05 SE (range = 1.4–1.6) chicks fledged annually from successful nests in the five years with ≥10 successful nests.

Using a general linear model, we evaluated tail length, age in days, and the year of hatching as categorical predictors of nestling weight at the time of banding (Figure 9.4). Our sample included 47 nestlings of known age (2 of 10 days, 6 of 13 days, 30 of 14 days, 6 of 15 days, 3 of 16 days). Significant predictors were tail length ($F_{1,37} = 112.6$, $P < 0.001$), year ($F_{4,37} = 23.3$, $P < 0.001$), and the interaction between year and tail length ($F_{4,37} = 4.0$, $P = 0.009$). Age in

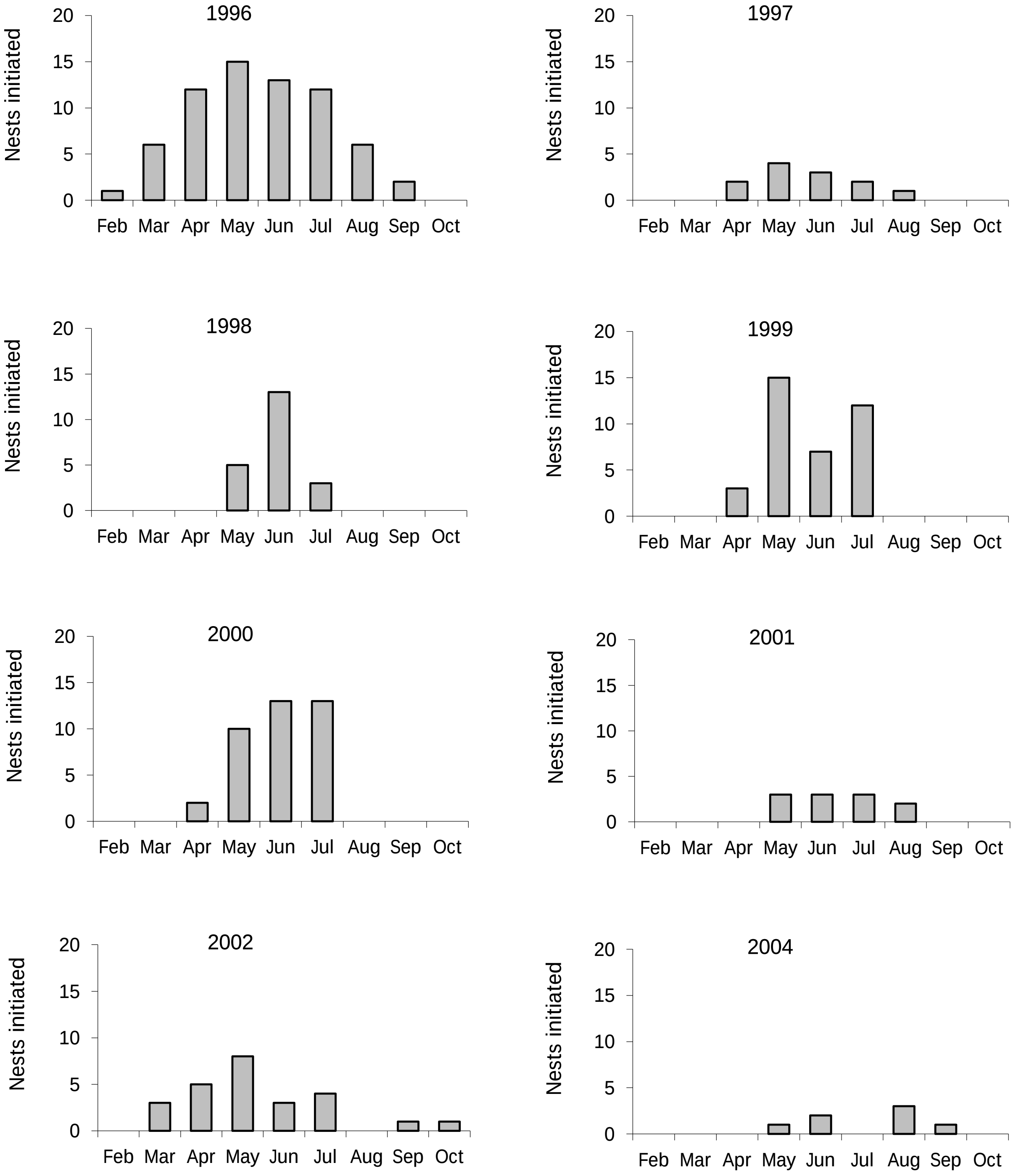

Figure 9.2. Number of active palila nests initiated each month on the western slope of Mauna Kea, Hawai‘i, 1996–2004. No active nests were found in 2003. In 2004, most nests were found late in the season due to a delay in systematic nest searching.

Table 9.4. Mean monthly number of māmane flowers from four months significantly predicted the number of nests found per km^2 during 1996–2003, based on a general linear model.

Month	Coefficient	*P* value
(Intercept)	0.383	0.062
September	0.001	0.003
April	0.005	0.007
March	-0.004	0.003
January	0.005	0.001

Table 9.5. Predicted and actual number of nests found within 50-m belt transects in 2004 for four palila study grid areas on the western slope of Mauna Kea, Hawai'i, based on data collected during 1996–2004.

Variables	Mauka	Makai	Ahumoa	Manao
2002 search area (km^2)	0.83	1.04	0.28	0.26
Predicted nests/km^2	6.05	1.29	4.73	0.81
Actual nests/km^2	8.6	8.2	6.3	19
Predicted nests 2004*	5.03	1.33	1.31	0.21

*Assuming same search effort as in 2002

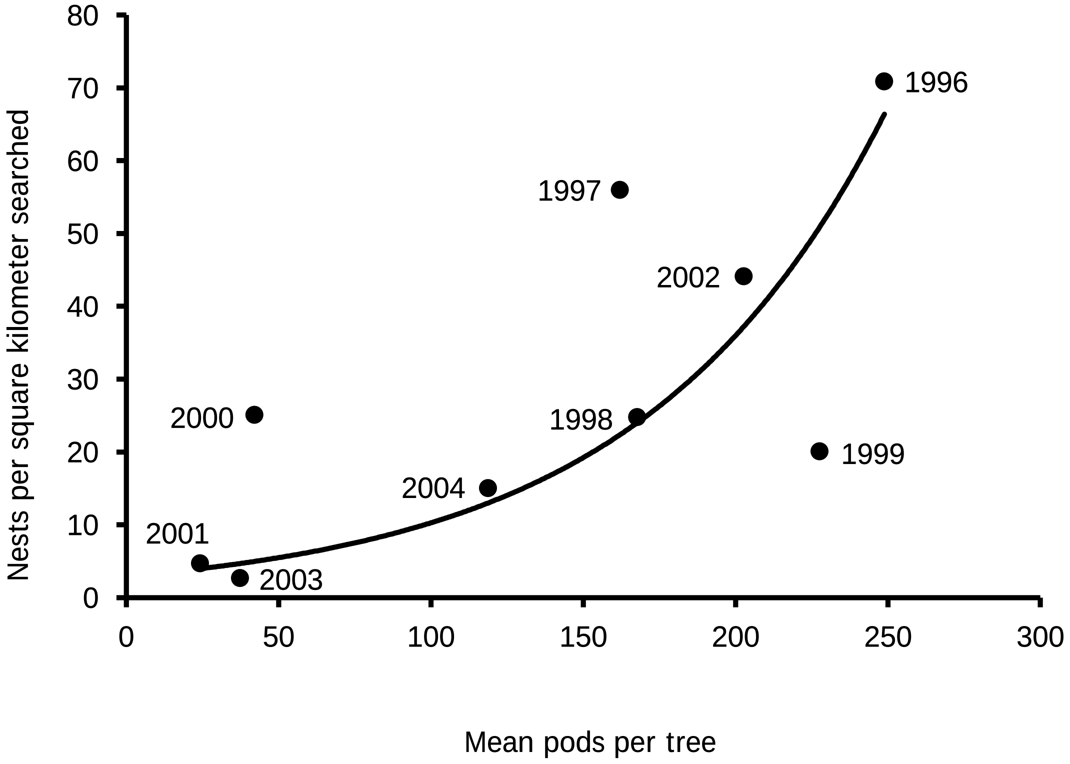

Figure 9.3. Exponential regression curve showing relationship between mean number of māmane pods during the breeding season (April–August) and nest density (active nests per square kilometer) on the western slope of Mauna Kea, Hawai'i, 1996–2004.

Table 9.6. Results from inactive palila nests found on the western slope of Mauna Kea, Hawai‘i, 1996–2004.

	No sign of hatching or chicks								Hatch or chicks evident		
Year	Total inactive nests	No sign of hatch or chicks	Incomplete construction	Empty	Clutch abandoned	Eggs broken	Adult depredated	Rat feces found	At least 1 egg hatched	Brood dead in nest	Fecal deposits on nest
1996	86	50/86	4/50	24/50	15/50	3/50	2/50	2/50	36/86	9/36	27/36
1997	45	28/45	0	24/28	1/28	1/28	1/28	1/28	17/45	2/17	15/17
1998	28	16/28	0	2/16	9/16	5/16	0	0	12/28	2/12	10/12
1999	32	12/32	0	5/12	2/12	5/12	0	0	20/32	3/20	17/20
2000	32	9/32	0	4/9	3/9	2/9	0	0	23/32	2/23	21/23
2001	6	3/6	1/3	2/3	0	0	0	0	3/6	1/3	2/3
2002	15	6/15	0	4/6	1/6	1/6	0	0	9/15	0	9/9
2003	5	2/5	0	2/2	0	0	0	0	3/5	0	2/3
2004	8	4/8	0	4/4	0	0	0	0	4/8	0	4/4

Table 9.7. Detailed monitoring results of active palila nests on the western slope of Mauna Kea, Hawai‘i, 1996–2004.

	1996	1997	1998	1999	2000	2001	2002	2004
Number of active nests	46	12	21	37	36	11	25	7
Unsuccessful (no chicks fledged)	19/46	8/12	9/21	15/37	12/36	9/11	11/25	3/7
Abandoned before laying	1/19	1/8	0	0	0	0	0	0
Clutch failed to hatch	8/19	1/8	2/9	6/15	5/12	6/11	4/25	1/3
Brood failed to fledge	7/19	6/8	7/9	9/15	6/12	3/11	5/25	2/3
Eggs disappeared	3/19	0	0	0	1/12	0	2/25	0
Successful (≥1 chick fledged)	27/46	4/12	12/21	22/37	24/36	2/11	14/25	3/7
1 chick fledged	17/27	3/4	7/12	10/22	9/24	1/2	9/14	1/3
2 chicks fledged	10/27	1/4	5/12	12/22	15/24	1/2	5/14	2/3
Outcome unknown	—	—	—	—	—	—	—	1

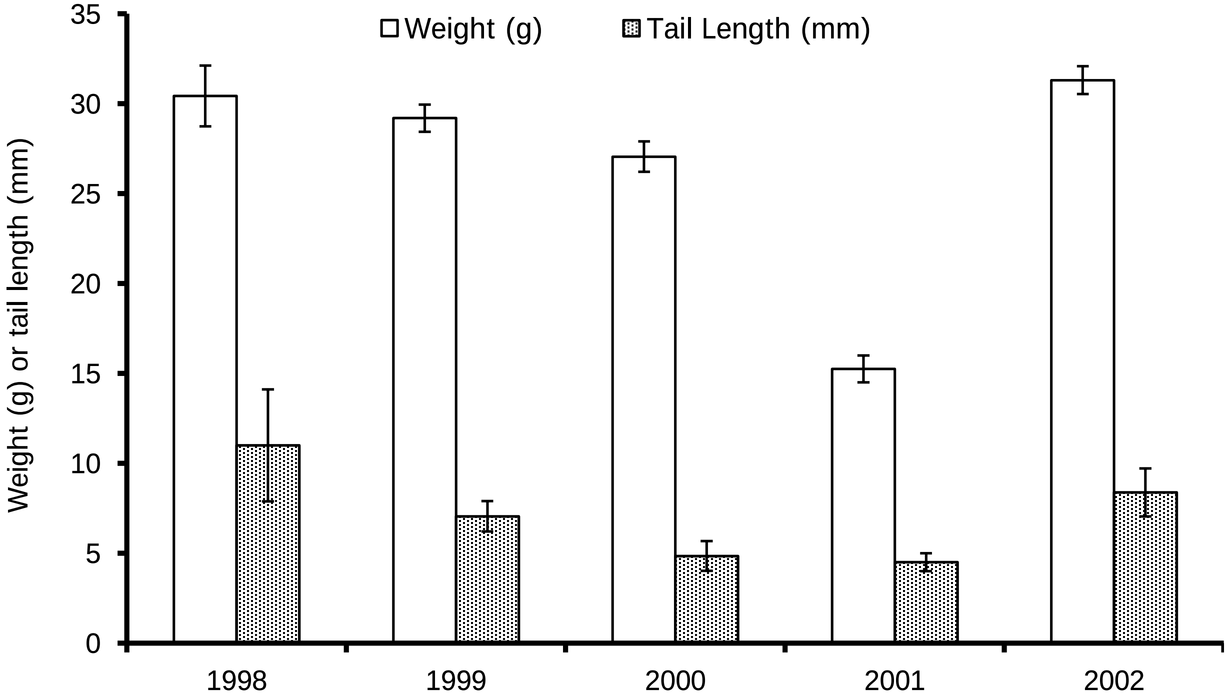

Figure 9.4. Mean weight (g ± SE) and tail length (mm ± SE) of palila nestlings (10–16 days of age) by year on the western slope of Mauna Kea, Hawai‘i, 1999–2002. No active nests were found in 2003.

days was not significant ($F_{4,33} = 0.7$, $P < 0.42$), nor were the other secondary and tertiary interactions.

The effect of tail length accounted for a 0.13-g increase in nestling weight for every mm of tail length. A post facto Tukey's HSD test of year effects (type I error = 0.10) revealed that, other factors being equal, nestling weights were significantly lower in 2001 than in 1999, 2000, and 2002, which drove the tail:year interaction. Nestling weights in other years were indistinguishable from one another.

Although variable, egg fertility was generally high each year (88 ± 6.4%; range = 75–95%; Table 9.8). Most (91 ± 8.2%; range = 75–100%) of the fertile eggs we monitored each season hatched, and over half (56 ± 21.0%; range = 22–100%) produced fledglings. Considering all eggs produced each season during 1996–2004, most produced hatchlings (66 ± 15.1%; range = 35–83%), and over a third produced fledglings (40 ± 12.8%; range = 18–55%; Table 9.9). The proportion of successful nests did not differ significantly among years (df = 7, $\chi^2 = 11.3$, $P > 0.2$).

Causes of Nest Failure

We monitored nesting activity using video surveillance at eight nests in 1999, four nests in 2000, three nests in 2001, and one nest in 2002. Eight of the 16 video-monitored nests were successful in fledging at least one chick. One nestling disappeared from each of two nests, although both nests fledged the remaining nestling. Causes of the nestling disappearance were

Table 9.8. Fertility of eggs from all active palila nests with a complete clutch (at least two eggs, one egg and one chick, or two chicks) on the western slope, 1996–2004, and northern slope, 2004, of Mauna Kea, Hawaiʻi.

Year	Total eggs	Fertility unknown	Fertile	Infertile
1996	99	12/99	79/87	8/87
1997	20	0	18/20	2/20
1998	37	4/37	29/33	4/33
1999	69	6/69	60/63	3/63
2000	64	5/64	55/59	4/59
2001	17	7/17	8/10	2/10
2002	50	15/50	32/35	3/35
2003	0	0	0	0
2004	6	2/6	3/4	1/4
North slope, 04	3	0	2/3	1/3

Table 9.9. Incidence of hatching and fledging from all active palila nests with a complete clutch on the western slope, 1996–2004, and northern slope, 2004, of Mauna Kea, Hawaiʻi.

	1996	1997	1998	1999	2000	2001	2002	2003	2004	North slope, 2004
Total eggs	99	20	37	69	64	17	50	0	6	3
Nestlings from all eggs	72/99	15/20	28/37	51/69	53/64	6/17	31/50	0	3/6	2/3
Fledglings from all eggs	48/99	4/20	15/37	32/69	35/64	3/17	19/50	0	3/6	Unknown
Fertile eggs	79	18	29	60	55	8	32	0	3	2
Nestlings from fertile eggs	72/79	15/18	28/29	51/60	53/55	6/8	31/32	0	3/3	2/2
Fledglings from fertile eggs	48/79	4/18	15/29	32/60	35/55	3/8	19/32	0	3/3	Unknown

not apparent on the video, but we found one of these nestlings at the base of the nest tree, possibly having fallen out during a storm (Table 9.10). This chick (18 days old) had bruising on its head, but massive congestion in the lungs suggested that it died from acute shock (T. Work, U.S. Geological Survey, personal communication). We did not locate the chick (7–10 days old) from the other nest. Feral cats (*Felis catus*) depredated four video-monitored nests when nestlings were 12–16 days old (two in 1999, one in 2000, and one in 2001). We recorded only two instances of predation by feral cats on video; once in 1999 and again in 2001. Due to a power failure at night in 1999 and equipment shutdowns on weekends in 2000, we did not obtain recordings of the other two instances of predation by feral cats. In 2001, two nestlings died in the nest and the cause of death was classified as pulmonary congestion (T. Work, U.S. Geological Survey, personal communication). Camera problems prevented us from determining what factors may have caused the deaths. Females abandoned their clutches at two video-monitored nests in 1999. One female abandoned her nest two days after camera placement. Observations from a blind and video surveillance did not implicate the camera as a cause for abandonment. The female attended the nest normally, and the male fed her regularly. At the other nest, the female abandoned her eggs during video camera introduction. We modified our camera introduction protocol subsequently to reduce the risk of abandonment.

Table 9.10. Storm-related palila nestling mortality on the western slope of Mauna Kea, Hawai‘i, 1999–2004.

Year	Stage	Number of eggs or nestlings	Natural event	Cause of death
1999	Nestling	2	Wind storm	Pulmonary congestion → shock
2000	Nestling	2	130 mm rain	Pooling of blood → shock
2001	Nestling	1	Hail storm	Nestling disappeared
2002	Egg	2	Spring storm	Abandoned
2002	Egg	2	Spring storm	Abandoned
2002	Nestling	1	Rain storm	Chick on ground below nest
2002	Nestling	2	Heavy rain	Pulmonary congestion→shock

In 2004, we observed eight nests from blinds without using video surveillance. On the western slope of Mauna Kea, nestlings from two nests fledged successfully, one nest was abandoned by the parents at the egg stage, nestlings from two nests died of unknown causes, and nestlings from one nest fledged prematurely during the nest monitoring procedure. On the northern slope, we found a nest of the captive-reared birds and a nest of the translocated palila (see Chapter 2: Translocating Wild Palila and Chapter 4: Release and Monitoring of Captive-reared Palila). The nest of the captive-reared birds contained only an infertile egg. The nest of the translocated wild pair produced two nestlings, but we were unable to determine whether the nestlings fledged.

Storms were associated with the failure of one nest each year during 1999–2001 and possibly four nests in 2002 (Table 9.10). Although necropsy results did not suggest infectious diseases or physical trauma as having contributed to the deaths of chicks in these nests, signs of shock were evident from pulmonary congestion and pooling of blood in some (T. Work, U.S. Geological Survey, personal communication). Severe pulmonary congestion related to acute stress or shock was noted in seven nestlings that died during 1999–2001, but factors causing the shock were not apparent. The cause of death also was unclear for two nestlings (13–14 days old) that died in 1999 with ample fat reserves and the appearance of being in excellent condition. Additionally, two 4-day-old nestlings found dead in 2000 seemed to be normal in size, but the yolk sac of one was leaking into the abdomen, possibly due to blunt trauma to the abdomen and possibly contributing to its death (T. Work, U.S. Geological Survey, personal communication). At a nest with two chicks under video surveillance in 2001, a 14-day-old chick was found dead, hanging upside down from the outside rim of the nest, and three days later, the second chick was also found dead in the nest. The second chick was found to have pulmonary congestion due to stress (T. Work, U.S. Geological Survey, personal communication), but the cause of the first chick's death was unknown. In 2002, we found a healthy week-old chick dead in the nest without any sign of disturbance to the nest, but a necropsy was not performed.

Many nestlings also disappeared from nests for unknown reasons (Table 9.11). Some may have been removed from the nest by an avian predator such as pueo (*Asio flammeus sandwichensis*). Pueo were observed flying near one failed nest on several prior occasions (see Chapter 2: Translocating Wild Palila).

Table 9.11. Unexplained palila nestling disappearance on the western slope of Mauna Kea, Hawai'i, 2000–2002.

Year	No. nestlings	Age (days) of nestlings at disappearance[†]	No. nestlings disappeared	No. nestlings fledged
2000	2	1	2	0
2000	2	7–12	1	1
2000	2	7–12	1	1
2000	2	7–12	1	1
2002	2	ND	1	1
2002	3	ND	2	1
2002	2	≤7	2	0
2002	2	7	2	0
2002	2	ND	1	1
2002	2	ND	1	1
2002	2	ND	2	0
2004	2	<7, <19	2	0

[†] ND = not determined

Disease was rarely found in the nestlings that died. Bacteria (*Escherichia coli*) were first implicated in the death of a nestling found at the base of the nest tree within a week of fledging in 2000 (T. Work, U.S. Geological Survey, personal communication).

Two nests failed at the egg stage in 2000. The first nest failed on day 15 of incubation. One broken eggshell and yolk were found on branches below the nest. The female was wearing a radio-transmitter and was found foraging within 300 m of the nest tree after the failure of her nest. The second nest was found empty three days after she had last been observed incubating. The nest material had been disturbed and several pieces of the nest were found on branches below. No eggshells were found below the nest.

In 2001, six nests failed at the egg stage. Two nests were abandoned shortly after being discovered, and two other nests were abandoned possibly due to storms. At the fifth nest, incubation of an egg with a dead embryo had proceeded for ≥18 days. The sixth nest was found disturbed with both eggs broken on the ground below the nest. Although there were no signs of depredation, game bird feces were observed on branches around the nest, suggesting that disturbance by a roosting game bird may have dislodged the eggs from the nest.

Five nests failed at the egg stage in 2002. Two nests were abandoned the day after being discovered. Two nests were abandoned following storms. Another nest failed due to infertile eggs, although the female incubated for ≥20 days.

Discussion

Palila nesting phenology varied greatly in duration and magnitude from year to year, presumably mostly in response to food availability (Banko *et al.* 2002b). We found a positive correlation between the number of active nests during the breeding season and the number of māmane pods available (Figure 9.3). Nevertheless, factors other than food availability also affected nesting effort. There were very few pods available in 2000, 2001, and 2003, likely due to drought (Banko *et al.* 2013; see Figure 5.5 in Chapter 5: Population Trends and Response to Environmental Factors), yet annual nest density varied substantially. We found the fewest nests in 2003, when drought conditions were severe (see Figure 5.6 in Chapter 5). Nesting started early in 2002, likely in response to an early and relatively abundant pod crop (see Chapter 16: Food Availability: Māmane Phenology). The number of pods per tree was higher in the spring of 2002 than in the previous three years, which may partly explain the peak of palila numbers in early 2003 (Banko *et al.* 2013).

Our model to predict the number of nests likely to be found in the breeding season based on flower abundance in the preceding months produced accurate estimates for 1998, 2001, and 2002. More palila nested in 2004 than the model predicted, especially in the naio-dominated forest areas (Manao and Ahumoa). The increased number of nests may have been stimulated by increased food following the abundant rains that broke the preceding 13-month drought (Banko *et al.* 2013). Additionally, the abundance of food six months or more before the breeding season also may influence nesting effort. The greater than predicted nesting activity observed in 1997 and 2000 may have been stimulated by increased food abundance in 1996 and 1999.

Incorporating the 2004 nesting season results produced a model with no significant predictors of nesting effort, suggesting that evaluating additional predictors could improve the model. The current model incorporated phenology data beginning with the September before the breeding season, but including phenology from more than a year in advance might refine the idea of a biological lag in bird breeding condition.

Palila breeding activity was largely driven by the availability of māmane pods (Pratt *et al.* 1997, Banko *et al.* 2009), and we found in seven of nine years that nest density was higher in māmane-dominated than it was in naio-dominated forest. Additionally, māmane-dominant forest was distributed at a higher elevation, making māmane seeds available earlier in the season (Banko *et al*. 2002c).

The annual percentage of palila nests in which eggs hatched varied relatively little during 1996–2004, suggesting that food availability and weather had little influence on egg viability overall. Nevertheless, the hatching rate was low in 2001, when drought and the scarcity of māmane pods (Banko *et al.* 2013) may have altered incubation behavior in ways that affected embryonic development. In 2002, with the return of wetter conditions, the hatching rate rebounded to typical levels.

Annual nest productivity varied somewhat more during the chick-rearing stage, although chicks fledged from over half the active nests in most years. There also may have been a lag effect of food abundance from the previous year in these cases. Fledging success in 2002 was high, but not as high as expected following cat removal from the palila nesting habitat (Hess *et al.* 2004; see Chapter 35: Impact of Predators on Bird Reproduction and Chapter 36: Predator Management).

Chicks were significantly smaller in 2001 compared to those in 1999, 2000, or 2002. Even so, two small chicks fledged in 2001, whereas their heavier siblings died of pulmonary congestion (T. Work, U.S. Geological Survey, personal communication). Thus, fledging success may not always be predicted by chick weight or feather development.

Pratt *et al.* (1997) reported the range of annual hatchability of palila eggs during 1989–1993 to be 54–66%, whereas we found the range of hatchability to be 64–83% for 1996–2000, 2002, and 2004. We consider the low hatchability (35%) observed in 2001 to be anomalous; 55% of all active nests were abandoned during the egg stage, perhaps in response to low food availability, and the sample of eggs available to be examined was small. The moderate range of egg infertility (5–25%) during 1996–2004 suggested that infertility is not a serious demographic problem (also see Banko *et al.* 2002b).

Similar to the range of annual nest success (39–55%) reported by Pratt *et al.* (1997) during 1989–1993, we found that 33–67% of nests were successful during 1996–2004 (excluding 2001). The rate of nest success for 2001 was lower (18%) in comparison to other years, but it falls within the range (11–77%) of mainland passerines (Martin 1989). Annual nesting success of the palila was similar to the 18–79% of the red crossbill (*Loxia curvirostra*), which like palila, belongs to the Carduelinae family, breeds largely in response to the availability of seeds (coniferous species), and rears its nestlings over a relatively long period (16–28 days; Cramp *et al.* 1994). Nevertheless, palila nestlings are exposed to predators and storms for a longer time (21–30 days) than most other passerines (van Riper 1980; Pletschet and Kelly 1990; Banko *et al.* 2002b).

In māmane-dominant forest, feral cats were responsible for ≤11% of nest failures annually (Hess *et al.* 2004; see Chapter 35: Impact of Predators on Bird Reproduction). Predation might have been undetected in many cases without the use of video surveillance (Laut *et al.* 2003). We observed no nest failure due to feral cat predation in 2002, suggesting that feral cat management improved palila breeding productivity. However, we suspect some nests were depredated by native raptors, specifically pueo (*Asio flammeus sandwichesis*). An investigation of raptor ecology within the range of the palila could help determine their level of impact.

Although we cannot explain all of the variability in annual palila productivity, in most years nesting effort was related to food availability, which was linked to māmane flower production early in the spring and perhaps in some years to the size of the pod crop in the preceding year. The ability of palila to nest vigorously in some years may help offset drought years with poor productivity (Lindsey *et al*. 1997, Banko *et al.* 2013). The availability of food during the breeding season may also affect nest success, although further research is needed to understand the underlying mechanisms and interactions among variables.

Factors responsible for the disappearance or death of chicks or the causes of pulmonary congestion in otherwise healthy nestlings were difficult to determine, even with video surveillance. The presence of *E. coli* in a chick in 2000 suggests that bacteria or other pathogens may occasionally affect palila. Hypothermia after abandonment may have caused acute stress or shock that resulted in lung congestion in nestlings from several nests. Additionally, exploring the toxic properties of māmane seeds (Banko *et al*. 2002a) may uncover implications for the health of nestlings.

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10 NEST SITE SELECTION

Steve J. Dougill, Luanne Johnson, Chris Farmer, Paul C. Banko

Introduction

The quality of nesting habitat is likely to contribute to the success of restoring palila (*Loxioides bailleui*) populations and may account for some of the annual variation in palila breeding effort and success (see Chapter 9: Breeding Phenology, Productivity, and Nesting Success). In particular, Pletschet and Kelly (1990) examined the structure and composition of nest sites and found that successful palila nests were located in more isolated māmane trees (*Sophora chrysophylla*) than were unsuccessful nests. The vegetation within the palila's range changed as māmane regeneration increased after 1980 as feral sheep (*Ovis aries*) and mouflon (*O. gmelini musimon*) were culled annually in subalpine Mauna Kea (Scowcroft and Conrad 1988, 1992; Hess *et al.* 1999), and vegetation has continued to change since Pletschet and Kelly's research in 1988 (Reddy *et al.* 2012). Additionally, vegetation structure may be influenced by the frequent episodes of severe drought that have occurred since earlier vegetation studies (Banko *et al.* 2009, 2013). The goal of this study was to determine whether palila nest success responded to changes in forest structure since the results of Pletschet and Kelly (1990).

Methods

We recorded vegetation characteristics of each active nest site at the end of the breeding season in 1999–2001, based on Pletschet and Kelly's (1990) study design. After identifying the factors that affected nesting success during 1999−2001, we reduced the number of variables measured in 2002 to include only factors that were close to significance in the 1999–2001 analysis (Table 10.1). In 2004, we again measured these variables for the two nests found on the northern slope of Mauna Kea, one from a translocated wild pair and the other from a captive-reared pair (see Chapter 2: Translocating Wild Palila).

We used logistic regression to model the major factors affecting the probability of nest success based upon the reduced 1999–2002 data set (S-Plus 2000, rel. 2). We used nest success or failure as a binary response variable. We tested the year, tree species, tree vigor, initiation month, and presence or absence of vines in the canopy as categorical predictors. We tested 16 continuous predictors: tree crown height, major and semi-major diameter, distance from crown base to ground, nest height above ground, nest distance from the top and horizontal distance from the center of the vegetation clump containing the nest, percent cover immediately above the nest, distance to the nearest foliage of neighboring tree, distance to the nearest base of neighbor tree, volume of *Stenogyne* vines in nest tree, volume of canopy overlap with neighboring trees, height from ground of lowest nest tree canopy, nearest neighboring tree stem and foliage, percent of canopy that overlapped with those of neighboring trees, and percent of canopy volume occupied by *Stenogyne* vines.

Results

A total of 112 nests were quantified during 1999–2004 on both the western and northern slopes (1999: n = 36; 2000: n = 36; 2001: n = 11; 2002: n = 27; 2003: n = 0; 2004: n = 2). Palila typically nested in māmane; however some nests were also found in naio (*Myoporum sandwicense*; Figure 10.1). We found a few palila nests in native shrubs such as pilo (*Coprosma montana*) and naʻe naʻe (*Dubautia arborea*). One pair unsuccessfully nested in a clump of velvet grass (*Holcus lanatus*) in 2000.

Table 10.1. Vegetation variables measured for analysis of palila nest success on Mauna Kea, Hawaiʻi, 1999–2002.

Measurements, 1999−2001	Measurements, 2002
Tree species	Tree species
Maximum height and width of canopy	Maximum height and width of canopy
Height of nest from ground	Height of nest from ground
Distance from center of nest to canopy above nest	Distance from center of nest to canopy above nest
Distance from center of canopy clump which contains nest to center of nest	Distance from center of canopy clump which contains nest to center of nest
Percent of vine species cover in canopy	Percent of vine species cover in canopy
Vigor of nest tree[1]	Vigor of nest tree[1]
Distance from nest to nearest canopy on horizontal plane	
Height of lowest canopy in each cardinal direction	Height of lowest canopy
Distance to nearest base of neighbor tree	Distance to nearest base of neighbor tree
Distance to nearest foliage of neighbor trees	Distance to nearest foliage of neighbor trees
Presence of vines within 1 m of nest in each cardinal direction	Presence of vine species in canopy
Percent cover within 0.5 m of nest in each cardinal direction	Percent cover within 0.5 m above nest
Percent cover within 0.5 m above and below nest	
Nest placement in tree (terminal, lateral, central)	
Density of live foliage of nest tree[2]	
Presence of other nests in tree	
Nest fate	Nest fate
	Canopy overlap with neighboring trees
	Month of nest initiation
	Status of nest at discovery (active, inactive, unknown)

[1] Scale-based measurement where tree vigor was rated in categories based on the percent of twigs with foliage (0−5%, 5−50%, 50−90%, 90−100%; see Chapter 25: Vegetation Survey in Palila Critical Habitat).

[2] Same categories as above to rate the density of foliage on live limbs

During the 2004 palila translocation trial (see Chapter 2: Translocating Wild Palila), a wild translocated pair of birds successfully nested approximately 1.5 km northeast of Hack Tower 1 on an ʻaʻā lava flow in an area of scrubby vegetation. This nest was in a pūkiawe (*Leptecophylla tameiameiae*) bush approximately 1.3 m above the ground. This nest successfully fledged two chicks.

One captive-reared pair, released in December 2003, built a nest approximately 75 m north of Hack Tower 1 (see Chapter 4: Release and Monitoring of Captive-reared Palila). When this nest

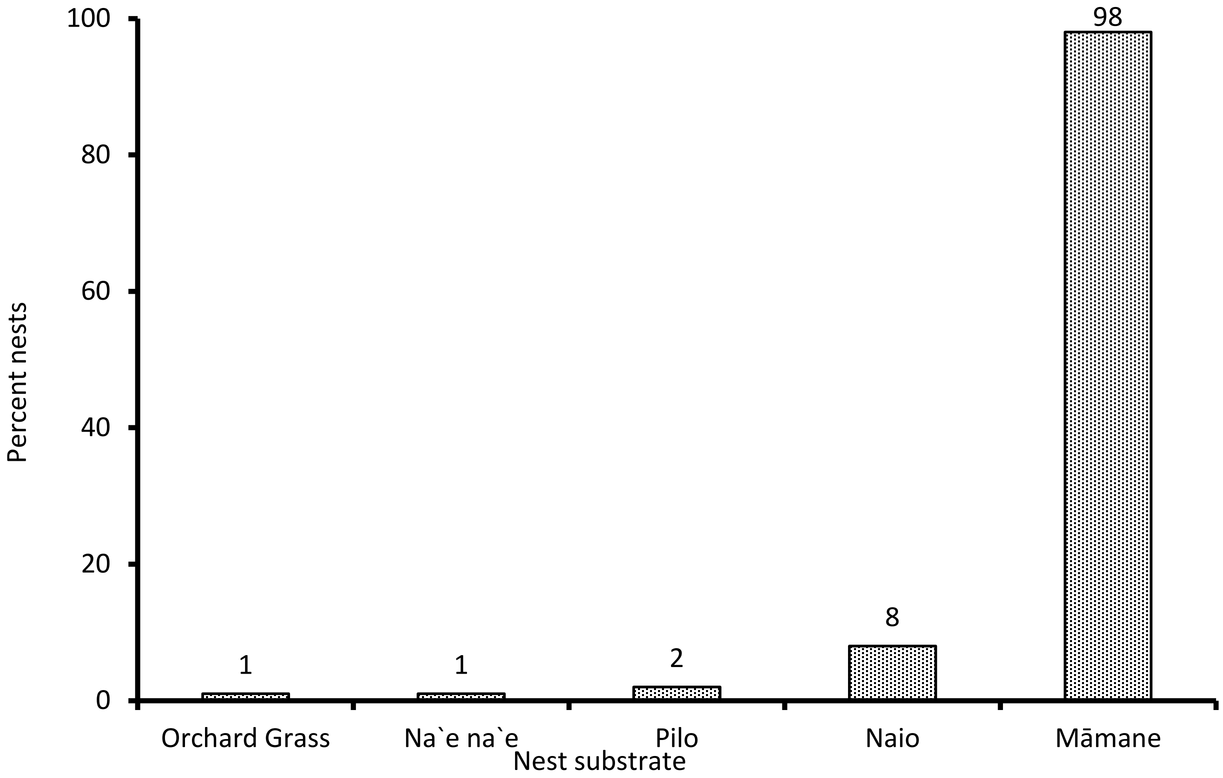

Figure 10.1. Percentage of active palila nests found in plant species on the western slope of Mauna Kea, Hawai'i, 1999–2002. The numbers of individuals of each plant species are indicated above the bars.

was discovered on 7 April 2004 it contained one egg. The female abandoned the nest by 10 April. The egg was later determined to be infertile. This nest was built approximately 1.5 m above the ground in a pūkiawe bush. This was the first nesting attempt by a captive-reared pair in the wild.

Since Pletschet and Kelly's (1990) study, several key components of palila nest sites have changed. The most noteworthy difference is finding the native mint *Stenogyne microphylla* associated with one-third of all active nests from 1999–2002 (*n* = 99). Pletschet and Kelly (1990) did not find any *Stenogyne* spp. associated with nests in their study. We found that the mean canopy area of māmane nest trees has increased over time, as well as the mean height of nest trees (Figure 10.2).

Using all our data, the logistic regression model identified four main effects and three interaction effects that were significant in identifying nest success or failure (Table 10.2). The significant main effects were year, the volume of tree canopy occupied by *Stenogyne* vines, the amount of canopy overlap with neighboring trees, and the distance to the nearest foliage (Tables 10.2, 10.3).

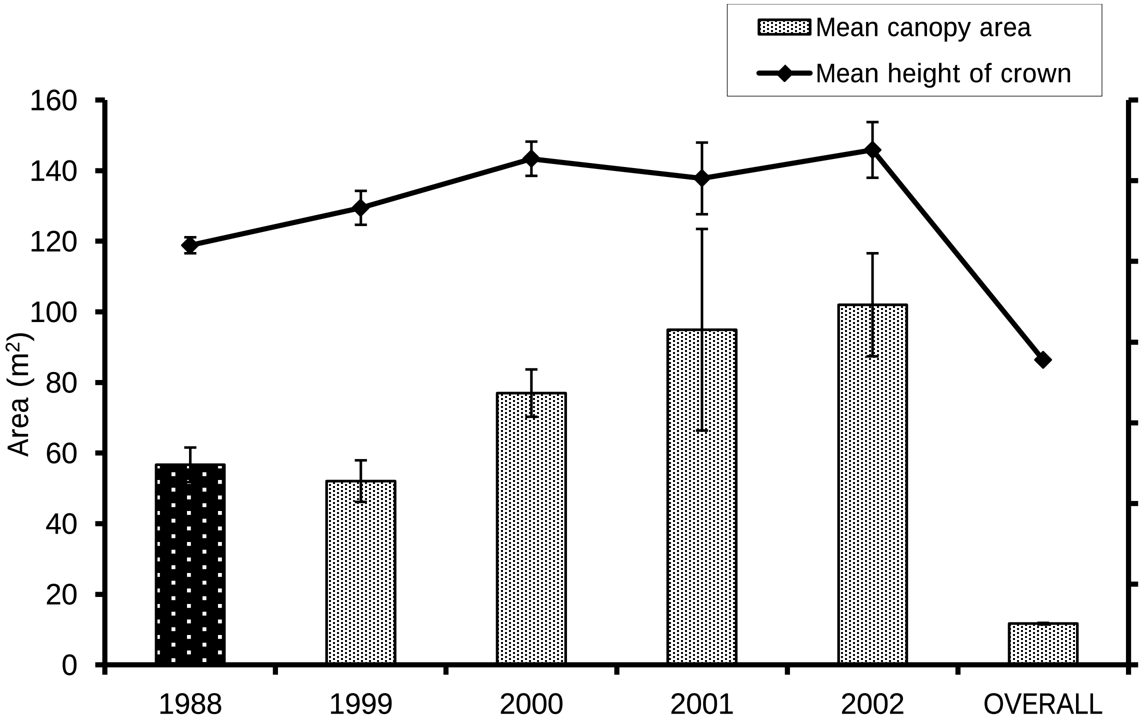

Figure 10.2. Mean area (m^2) of canopy (± SE) and mean crown height (m) of māmane trees (± SE) containing active palila nests compared to the paired sample of māmane trees ("overall") on the western slope of Mauna Kea, Hawai'i. Since 1988 (black bar; Pletschet and Kelly 1990), the size of nest trees has increased based on vegetation surveys conducted during 1999–2001.

Table 10.2. Analysis of deviance for the logistic regression model identifying the important vegetation characteristics associated with nest success of palila on Mauna Kea, Hawai'i, 1999–2002. Significant effects at alpha = 0.10 are indicated by *.

Effect	df	χ^2 probability
Year*	3	0.033
Nest height	1	0.418
Stenogyne volume*	1	0.029
Canopy overlap*	1	0.060
Lowest canopy height	1	0.106
Distance to nearest foliage*	1	0.077
Nest height: nearest foliage*	1	0.043
Stenogyne: lowest canopy*	1	0.074
Year: nearest foliage*	3	0.032

Discussion

We found that the native mint, *Stenogyne microphylla*, was an important component of palila nest success not reported by Pletschet and Kelly (1990). Foliage of this plant may be important

Table 10.3. Coefficients of predictors associated with nest success of palila on Mauna Kea, Hawai'i, 1999–2002. Positive values indicate an increase in the probability of nest success; negative values indicate a decrease. Significant effects are indicated by *; $P < 0.1$.

Effect	Value	Standard error	t-value	*P*
(Intercept)	0.844	1.022	0.826	0.4112
Base (1999)	0.000	—	—	—
Year1 (2000)*	1.089	0.435	2.501	0.0143
Year2 (2001)*	-0.753	0.403	-1.871	0.0648
Year3 (2002)	0.122	0.175	0.696	0.4881
Nest height from ground	-0.053	0.227	-0.235	0.8144
Volume of *Stenogyne* in nest tree*	0.128	0.061	2.103	0.0384
Volume of canopy overlap with neighboring trees*	-0.055	0.023	-2.402	0.0185
Height from ground of lowest nest tree canopy	-0.723	0.676	-1.070	0.2877
Distance to nearest foliage of neighboring tree*	-4.403	2.574	-1.711	0.0908
Nest height: nearest foliage*	0.367	0.159	2.312	0.0232
Stenogyne volume: lowest canopy*	-0.409	0.211	-1.933	0.0565
Year1: nearest foliage*	-0.369	0.177	-2.078	0.0407
Year2: nearest foliage	0.065	0.166	0.394	0.6943
Year3: nearest foliage	-3.034	2.434	-1.247	0.2160

when tree foliage is sparse, such as during drought conditions. It is possible the droughts of 1998 and 1999 affected foliage density of māmane in 1999, causing palila to select trees containing *S. microphylla* for greater cover near their nests.

Trees selected for nesting by palila during 1999−2004 had larger canopies and were taller than those in Pletschet and Kelly's (1990) study (Figure 10.2). This suggests that palila select larger trees for nest sites if they are available; nevertheless, large māmane are still uncommon in many areas of Mauna Kea (Banko *et al*. 2009). This may be an important consideration for planning reintroduction or forest restoration (see Chapter 26: Vegetation Surveys on Mitigation Parcels). The increase in larger nest trees likely reflects growth, but is perhaps also a response to ungulate culling since 1980. Habitat degradation by feral ungulates was a major factor in the decline of palila and has hindered their recovery (Scott *et al*. 1984; Banko *et al.* 2009, 2013). Eliminating browsing ungulates entirely from palila habitat would speed forest recovery and increase the availability of preferred nest sites.

Palila primarily nested in māmane trees, but other species were used for approximately 10% of nests. The fact that palila did not nest exclusively in māmane, but selected a range of species including trees, shrubs, and grasses, suggests they may have used a much wider range of nest sites before the composition of the forest was altered by ungulate browsing.

The results of our nest site model provided some insights about the outcome of palila nests. As it related to nest-site selection, year was likely confounded by other variables such as food resources, weather, and productivity during the previous breeding season. The volume of *Stenogyne* vines was significantly and positively related with nest success perhaps because they provided cover and nest material, especially during years of drought when māmane trees were sparsely foliated. Palila also eat the buds, flowers, and young leaves of *Stenogyne*, which may have been important alternate foods in years of low māmane pod production.

The amount of canopy overlap with neighboring trees resulted in a negative relationship with nest success, possibly because branches of neighboring trees increase the number of routes available to nest predators, such as rats and cats. On the other hand, we found that nest success also decreased with distance to nearest neighbors, suggesting that adjacent trees can provide additional cover from adverse weather and may help hide nests from aerial predators, such as owls. In this respect, our results contrast with Pletschet and Kelly (1990), who found that nest trees isolated from neighboring trees proved to be more successful. The optimal amount of foliage overlap may change between years, depending on the specific year's trade-off between cover and predation risk.

Another negative relationship with nest success was the combination of *Stenogyne* volume and the lower height of the canopy of the nest tree. Even with the seemingly beneficial effect of the native mint, the lower level of the canopy and tangle of vines may have enhanced access to the nest by predators. However, these two factors may be confounded if the effects of *Stenogyne* and crown height are affected by some common, unmeasured variable, such as microclimate.

Despite the overall homogeneity of palila nesting habitat at the landscape scale, palila select vegetative characteristics at the microhabitat scale for their nesting substrate. As the subalpine habitat recovers from decades of browsing, the quality of nesting habitat should improve.

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11 BEHAVIOR AT NESTS

Megan E. Laut, Elizabeth M. Gray, Paul C. Banko

Introduction

Video surveillance of nests is a relatively common technique used to identify nest predators (Thompson *et al*. 1999, Farnsworth and Simons 2000, Pietz and Granfors 2000); however, few studies of birds have utilized video cameras to quantify parental behavior (but see Cartar and Montgomerie 1987, Challet *et al*. 1994, Proudfoot and Beasom 1997, Delaney *et al*. 1999). Video recordings allow researchers to collect more precise behavioral data than via nest-blind observations because of the ability for repeat viewings. For example, the movement of young chicks in the nest can be recorded with video, but usually not observed from a blind. Additionally, observer interference is reduced since the nest is not approached during data collection. Quantifying parental care in endangered species can aid in the recovery of these species, especially in cases where nest failure has been identified as a source of population decline. We studied the nesting behavior of the endangered palila (*Loxioides bailleui*) using time-lapse videography to quantify parental behavior (also see Laut *et al.* 2003). We later used near real-time (six frames per second) videography to document palila nesting behavior (U.S. Geological Survey unpublished data). Those VHS recordings were digitized, but the results were not analyzed due to the large volume of data and low likelihood of adding measurably to our knowledge of palila nesting behavior.

Several studies of palila nesting behavior have been conducted from blinds (van Riper 1978, 1980; Pletschet and Kelly 1990; U.S. Geological Survey unpublished data) from which basic biological information was collected. Although there are records of palila breeding throughout the year, the vast majority of nesting occurs between March and September with the peak number of nests initiated in June (see Chapter 9: Breeding Phenology, Productivity, and Nesting Success). A median of two eggs is laid per clutch (range = 1–3 eggs), and the nest cycle lasts an average of 42 days from the initiation of incubation to fledging (Pletschet and Kelly 1990, Banko *et al.* 2002). Nesting success ranges from 39–55% with hatch failure as the main cause of nest mortality (Pratt *et al*. 1997a). Of nests that succeed in hatching, 52–66% fledge at least one nestling (Pratt *et al*. 1997a). Fledgling care lasts at least 30 days and up to four months (Miller 1998), thereby limiting the number of clutches a pair can successfully raise in any one season.

Palila are monogamous breeders, although some breeding pairs have secondary male helpers attending the nest during both the incubation and nestling stages (Pratt *et al*. 1997a, Miller 1998). The genetic relationship of secondary males to the nesting pair is stronger than to birds at large in the population (Patch-Highfill 2008; see Chapter 8: Breeding Demography), and no evidence of extra-pair fertilization has been found (Fleischer *et al*. 1994). A male-biased sex ratio in adults has been documented (Lindsey *et al*. 1995; see Chapter 6: Sex Ratio), which might explain the occurrence of helper males. The typical age at first breeding is two years for females and three years (or more) for males (Pratt *et al.* 1997a, Banko *et al.* 2002).

Fourteen of the 24 remaining species of Hawaiian honeycreepers (Fringillidae, Drepanidinae) are endangered (Pyle 1997) and many are likely extinct (Gorresen *et al*. 2009). Because the reproductive success of all honeycreeper species is influenced by the same ecological factors, information from our research could be applicable to the conservation of other Hawaiian honeycreepers. Nest chronology and success have been investigated in most of these species, but little information about their incubation behavior exists. This absence of data is due to the difficulty in accessing the rugged, remote areas where these birds remain, finding nests of rare species, and observing their behavior at nests in tall trees or cavities. Characterization of palila nesting behavior through the use of video recordings may help identify situations that can be solved with management, including intervening at nests with high potential to fail.

Methods

We conducted this study during the breeding seasons of 1991, 1993, and 1994. Nests were located by searching along transects within two established study grids on the western slope of Mauna Kea, Hawai‘i. The dominant vegetation at the upper elevations (>2300 m) within both study grids is open-canopy māmane (*Sophora chrysophylla*)-dominant forest with a mainly grass understory, which grades into māmane-naio (*Myoporum sandwicense*) mixed forest at elevations below 2300 m. All of the nests in this study were located in the māmane-dominant forest. The average daytime temperature is 11°C, with nighttime temperatures sometimes several degrees below 0°C. The climate is dry with average annual rainfall ranging from 35–75 cm (Juvik *et al*. 1993). Significant *El Niño* effects occur with a drastic decrease in rainfall. In such years, fewer pairs attempt to nest and overall breeding effort is severely reduced (van Riper 1980, Lindsey *et al*. 1995, Lindsey *et al*. 1997).

A black and white video camera with an external infrared illuminator connected to an 8-mm Sony video recorder set at 10-second intervals was introduced to each nest over one-to-two days. The 5x7x13 cm camera was placed approximately 30 cm from the nest cup. Nests were recorded continuously (day and night) until the nestlings fledged or the nest failed. All videos contained a time/date stamp and nest identification. Each nest was visited approximately once every three days for regular nest-checks and to change the videotape.

Videos were watched on a black and white monitor using a multi-speed video player. The identity or gender of the focal bird was often not determined because color leg bands and plumage differences were not identifiable due to black and white film, camera angle, or image quality. We classified all adult birds sitting on the nest as females, since males of this species do not incubate. Adult behaviors were defined as follows: (1) *attentive*: female incubating eggs or brooding nestlings, (2) *recess*: female not on the nest, and (3) *visit*: adult (female or male) on or near the rim of the nest within the camera’s view. Visits were classified as feedings when an adult’s bill reached toward a nestling’s bill. Attempts to determine the gender of the feeding adult were made whenever possible, but in most cases the gender of the adult was indeterminate, and all data were analyzed with females and males grouped. Additional behavioral data (e.g., position changes, egg turning) were collected while the female was on the nest, but are not included in this analysis.

We compared the nest attentiveness of the female, the frequency of her incubation and brooding recesses, length of her incubation and brooding recesses, and provisioning rates by the male during incubation and by the male and female during chick rearing. For all tests we divided the nestling period into two stages: early (≤14-day-old chicks) and late (>14-day-old chicks). We chose 14 days because in the Laysan finch (*Telespiza cantans*), a related bird with a nestling period of similar length, growth rate is highest at day 14 (Morin 1991). Additionally, palila chicks are well-feathered and can thermoregulate around this time (van Riper 1978). A nest was excluded from analyses in cases where <50 minutes were recorded in an hour (for hourly averages or rates) or <650 minutes were recorded for daylight hours (for daily averages). We used one-tailed t-tests for all statistical analyses, applying Rice's (1988) correction for multiple comparisons where applicable.

Results

We observed seven nests over three years; two nests were observed only during the egg stage, two nests were observed only in the nestling stage, and three nests were recorded during both stages. We collected 742 hours of data during the egg stage and 1335 hours during the nestling stage. An average of 13.8 complete days (range = 3–25 days) was recorded at each nest during the nesting period. Each of two nests observed during only the egg stage had two eggs, of which only one hatched. A feral cat (*Felis catus*) depredated one nest on day two of the nestling stage. No helpers were identified at any of the nests in this study through observation from blinds, mist-netting at the nests, or video observation.

Female Nest Attendance

Females spent a greater percentage of daylight hours on the nest during the egg stage than the nestling stage (t = 2.62, *P* = 0.016; Table 11.1). This difference occurred due to a reduction in time spent on the nest in the late nestling stage. Females spent the same amount of time on the nest in the egg stage and early nestling stage (t = 1.60, *P* = 0.074), but the amount of time females spent on the nest was greater for the egg stage than the late nestling stage (t = 5.00, *P* < 0.001). Likewise, females spent more time on the nest in the early nestling stage than in the late nestling stage (t = 2.59, *P* = 0.019).

Table 11.1. Averages (SE) for palila parental attendance and behavior at seven nests on Mauna Kea, Hawai'i, as assessed by video recordings. Means with the same superscript are not significantly different using t-tests and adjusting *P*-values using Rice's (1988) correction.

	Egg stage (*n* = 5)	Nestling stage[1] (*n* = 5)	Early nestling stage[1] (*n* = 5)	Late nestling stage[1] (*n* = 4)
Attendance (% daylight)	82.3^{a} (3.6)	44.8^{b} (13.9)	63.2^{a} (11.4)	20.8^{c} (11.8)
Recess length (minutes)	4.5^{a} (0.8)	26.6^{b} (8.8)	12.3^{a} (4.6)	45.9^{c} (11.3)
Recess frequency (per hour)	2.0^{a} (0.1)	2.2^{a} (0.1)	2.7^{b} (0.2)	1.6^{c} (0.1)
Adult visits (per hour)	–	–	1.8^{a} (0.3)	1.6^{a} (0.5)

[1] No comparisons were made between the nestling stage and the early nestling or late nestling stage.

Nest Recess Length

Average recess length was significantly shorter during the egg stage than it was during the nestling stage (t = 2.50, *P* = 0.018). As with attendance, this effect did not take place until the late nestling stage. The length of nest recesses was the same for the egg stage and the early nestling stage (t = 1.67, *P* = 0.067), but was greater in the late nestling stage compared to either the egg stage (t = 3.67, *P* = 0.002), or the early nestling stage (t = 2.76, *P* = 0.010).

Nest Recess Frequency

The average number of nest recesses per hour was similar for the egg stage and nestling stage ($t = 1.27$, $P = 0.105$). Recesses were taken less frequently during the egg stage than the early nestling stage ($t = 3.99$, $P < 0.001$). However, a greater number of recesses were taken in the egg stage compared to the late nestling stage ($t = 4.44$, $P < 0.001$) and in the early nestling compared to the late nestling stage ($t = 6.27$, $P < 0.001$).

Visitation Rates

The average number of visits per hour by adults did not vary between the early and late nestling stages ($t = 0.39$, $P = 0.35$). On average, adults visited the nest fewer than two times per hour, regardless of nestling age.

Recess Pattern

Diurnal patterns for frequency or length of nest recesses did not vary with the stage of the nest or time of day (all $P > 0.05$). Regardless of the stage of the nesting cycle, females took the same number of recesses in each hour of the day.

Discussion

Attendance and Recesses

Of all the nesting stages, female palila are most attentive during the egg stage. This could be due to embryos' greater sensitivity to changes in temperature than nestlings, and because the male is able to provision the female more frequently before eggs hatch. Attendance decreased during the nestling period because recess length increased greatly over time. By day 15, palila chicks are well-feathered and are capable of independent thermoregulation (van Riper 1978); female recess length in this study increased substantially at day 17. Van Riper (1978) and Pletschet and Kelly (1990) found that females fed nestlings more often than did males. The need to simultaneously brood chicks and supply food explains why females recessed more frequently but for brief periods during the early nestling period. Studies of other Hawaiian honeycreepers reveal that females provision young more frequently than do males, especially in the first few days after hatching (Eddinger 1970, Lockwood *et al*. 1994, Kepler *et al*. 1997, Pratt *et al*. 1997b, Simon *et al*. 2000).

Visitation Rates

In our study, the average number of adult feeding visits did not change as nestling age increased, but Pletschet and Kelly (1990) found that rates of feeding decreased later in the nestling stage. The rate of feeding we observed throughout the nestling period was similar to the lower rate they reported for the late nestling stage. Differences in sampling method could explain these contrasting results: they observed nests for one-to-two hours every other day from a blind placed 10 m from the nest, whereas our observation was nearly continuous. Additionally, they could have classified parental visits where no chick feeding occurred as feeding events, thereby inflating estimates of feeding rates. On multiple occasions in our study, females returning from recesses looked into the nest, but did not feed nestlings before beginning to brood. The heads of young nestlings are not visible over the rim of the nest, so we could seldom determine whether or not food was transferred. Additionally, we could have missed feeding events that were contained within the 10 second gap in filming, although this is unlikely since most feeding events were >20 seconds. Comparison of field notes and real-time video observation of palila nests from the 1999 breeding season revealed that observers in blinds overestimated feeding rates because their views of the nest were obstructed or because the parents visited the nest very briefly without feeding nestlings (U.S. Geological Survey unpublished data).

Other studies of parental care show increased rates of feeding or increased food load by parents until just before fledging (e.g., Bedard and Meunier 1983). Growth rate of palila nestlings is slower than that for passerines of similar mass, which is probably due to the low rate of provisioning (van Riper 1980). Species with low predation risk grow more slowly and have longer periods of parental care while still in the nest (Ricklefs 1976). The long nesting cycle of palila could be attributed to the lack of mammalian predators in their evolution and also to the palila's relatively specialized diet (van Riper 1978). Compared to other honeycreepers, the palila's nesting cycle is long with respect to both the egg stage and the nestling stages (Simon *et al*. 2000, Banko *et al.* 2009, Woodworth and Pratt 2009), but is very similar to one of their closest relatives, the Laysan finch. However, Laysan finch nestlings fledge on average three days earlier than palila nestlings. Since the birds are of similar adult mass, the faster growth and earlier fledging date of the Laysan finch could be partly attributable to a diet more variable than the palila's (Morin 1991).

Rates of food delivery to nestlings are known for several species of Hawaiian honeycreepers (Eddinger 1970; van Riper 1978, 1980; Lockwood *et al.* 1994; Kepler *et al*. 1997; Simon *et al.* 2000). Of these species, palila have the lowest rate of delivery for both early and late nestling phases. Feeding rates of chicks may play a major role in determining the length of the nestling phase, but this can be tested only when more data are available for other Hawaiian honeycreepers. Food loads are not known for any species.

Palila eggs and nestlings must be protected from low temperatures at night and high levels of solar radiation during the day. Physiological changes in eggs allow for adaptation to cold temperatures, whereas adjustment to heat stress is dependent on the behavior of attending adults (Zerba and Morton 1983). Since palila are relatively heat intolerant (Weathers and van Riper 1982) and evolved in the absence of ground predators, their nesting behavior is more likely to be influenced by temperature and thermoregulatory limits of adults and nestlings. If heat stress affected parental behavior in palila, we would expect to see diurnal patterns in nest attendance. No behaviors associated with heat stress (e.g., panting) were observed for females at any of the nests. The lack of diurnal patterns in this study could potentially be attributed to the location of the nest in the tree, and we are investigating nest placement and the composition and structure of surrounding vegetation (see Chapter 10: Nest Site Selection).

Study Implications

Depredation rates likely could be underestimated at nests without video surveillance. The cause of failure of the cat-depredated nest in this study was initially attributed to a storm. The cat was at the nest less than two minutes; field notes indicate that the nest was not disturbed in any way, nor was there other evidence such as blood or body parts that could have indicated to investigators the true fate of the nest.

Technical problems made data collection difficult for portions of this study. Tape quality was poor in many instances, and black and white recording prevented adult identification by color leg band combinations.

Video cameras are useful in quantifying activity at nests and can be more clearly interpreted than information collected through observations in blinds. If audio recording is incorporated into the surveillance, vocalizations and activity in the vicinity of the nest can be analyzed (e.g., male called before female left the nest). Our study provides an introduction to understanding the variability of nesting behavior in palila at different stages of the nesting cycle. As part of a large, long-term study of palila breeding ecology, we expect that data collected from the continuing video surveillance in conjunction with information about the breeding pair (e.g., age, past breeding history) will help us to identify nests that have high potential to fail and determine causes of nest failure.

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SECTION III: HABITAT USE AND FOOD ECOLOGY

Preface

Due to the palila's extreme dependence on māmane seeds, its survival critically depends on the availability of food and quality of habitat. How far palila range and the habitats they occupy to meet their short-term and long-term needs is the topic discussed in Chapter 12. In Chapter 13, we report in detail on patterns of habitat use and foraging behavior with particular attention to the proportion of time spent feeding in māmane and other trees. Although it has long been known that māmane seeds are the main food of palila, in Chapter 14 we investigate the prevalence of *Cydia* caterpillars, which are found inside māmane pods, and other foods in the diets of birds according to their age and sex. We investigated the nutritional value and level of potentially toxic secondary compounds in māmane seeds in Chapter 15 to help understand why palila may be selective in their choice of trees in which to forage and their use of alternate foods such as caterpillars. Some of these results were published in 2002 (Banko *et al.* in Journal of Chemical Ecology 78:1393–1410).

We report on the seasonal and annual availability of important palila food resources in three chapters: māmane seeds and *Cydia* caterpillars (Chapter 16), caterpillars found on foliage (Chapter 17), and insects found on māmane trees in the Pu'u Mali mitigation parcel (Chapter 18). Given that *Cydia* caterpillars are found only inside māmane pods, they are exclusively available to palila and parasitoid wasps. We reared caterpillars to determine the prevalence of parasitism by native and introduced wasps and learned that the risk of being parasitized decreased with elevation. These results, reported in Chapter 19, were published in 2002 (Brenner *et al.* in Pan-Pacific Entomology 28:101–109) and 2004 (Oboyski *et al.* in Journal of Insect Conservation 8:229–240). Parasitism also affected caterpillars found on foliage, as described in Chapter 20. Additionally, invasive predacious insects attack the insect prey of palila, and we conducted surveys of yellowjackets (*Vespula pensylvanica*; Chapter 21), ants (Chapter 22), and a ground beetle (*Laemostenus complanatus*; Chapter 23) to assess the degree of threat.

Chapter 12. Habitat Use, Home Range, and Movements. Chris Farmer, Kevin W. Brinck, Luanne Johnson, Steven C. Hess, Steve J. Dougill, Paul C. Banko

Chapter 13. Habitat Use and Foraging Patterns. Steven C. Hess, Paul C. Banko, Linda J. Miller, Leona P. Laniawe

Chapter 14. Diet. Peter T. Oboyski, Paul C. Banko, John W. Slotterback

Chapter 15. Food Chemistry. Paul C. Banko, Kevin W. Brinck

Chapter 16. Food Availability: Māmane Phenology and Cydia Caterpillars. Peter T. Oboyski, Paul C. Banko, Luanne Johnson, Kevin W. Brinck

Chapter 17. Food Availability: Foliar Caterpillars. John W. Slotterback, Peter T. Oboyski, Paul C. Banko

Chapter 18. Food Availability: Insect Surveys in the Pu'u Mali Mitigation Parcel. David Pollock, Paul C. Banko

Chapter 19. Threats to Food Resources: *Cydia* Caterpillar Parasitism. Peter T. Oboyski, Paul C. Banko

Chapter 20. Threats to Food Resources: Foliar Caterpillar Parasitism. John W. Slotterback, Peter T. Oboyski, Paul C. Banko

Chapter 21. Threats to Food Resources: Yellowjackets. Kevin W. Brinck, Peter T. Oboyski, John W. Slotterback, Chris Farmer, David M. Pollock, Paul C. Banko

Chapter 22. Threats to Food Resources: Ants. Chris Farmer, Marla Schwarzfeld, Peter T. Oboyski, David M. Pollock, John W. Slotterback, Kevin W. Brinck, Paul C. Banko

Chapter 23. Threats to Food Resources: Predacious Ground Beetle. John W. Slotterback, Paul C. Banko

12 HABITAT USE, HOME RANGE, AND MOVEMENTS

Chris Farmer, Kevin W. Brinck, Luanne Johnson, Steven C. Hess, Steve J. Dougill, Paul C. Banko

Introduction

The endangered Hawaiian finch (Fringillidae: Drepanidinae), palila (*Loxioides bailleui*), occurs only in subalpine woodland on Mauna Kea Volcano, Hawai'i Island, and is the only remaining endemic bird that requires dry forest (Scott *et al.* 1986, Banko *et al.* 2009). Habitat use is one of the most important and relevant issues for the conservation of the palila because browsing by ungulates has degraded Palila Critical Habitat, resulting in range contraction and population decline (Banko *et al*. 2009, 2013). Understanding how palila use habitat on the western slope of Mauna Kea, where the birds are concentrated, can help develop management strategies in the short- and long-term. Analyses of home range can provide valuable information that, when used in combination with habitat use and food availability, can greatly aid in planning population reintroductions through the translocation of wild birds and releases of captive-reared birds. Additionally, identifying movement patterns and understanding daytime activity and nighttime roosting behavior can reveal habitat preferences as well as vulnerabilities to predators, which may have important management implications. Moreover, location data can reveal important distinctions in the habitat selection of a species due to variables such as age, sex, and breeding status.

Radio telemetry has been used in many forest bird studies to determine home range size, habitat utilization, and daily movement behavior (White and Garrott 1990, Millspaugh and Marzluff 2001). We radio-tagged palila during 1997–2005 on the western, eastern, and northern slopes of Mauna Kea, although these did not represent replicate populations. During the same period, we captured palila on the western slope and translocated them to the northern slope in an attempt to found a new population (see Chapter 2: Translocating Wild Palila). Radio-tagged palila included breeding adults, non-breeding adults, hatch-year, translocated, non-translocated, and captive-reared birds. Our overall goal was to determine whether variation in habitat use or movements might indicate important differences in habitat quality between sites or in the behavior of palila due to age, sex, breeding status, or management treatment.

Methods

As part of our comprehensive study of palila, we attached radio transmitters to 246 birds of all age classes and sexes for a wide range of research goals from 1997–2005. The majority of our research occurred on the western slope of Mauna Kea, although a significant component consisted of studying birds translocated to the northern slope. Birds were captured and radio-tagged at various banding stations on the western slope of Mauna Kea, with additional birds captured at active nest sites. Palila were released on the western slope after processing if they appeared too stressed, were recaptured after returning to the west slope within that year, were in breeding condition, a mate was present at the net but not captured, or due to old age. We tracked birds throughout the year.

The five translocations occurred in February–May 1997 (T1), October 1997–May 1998 (T2), November–December 1998 (T3), April 2004 (T4), and March–April 2005 (T5; see Chapter 2: Translocating Wild Palila). Additionally, Keauhou Bird Conservation Center released 10 captive-reared birds in December 2003 and 5 captive-reared birds in December 2004 onto the northern slope, and we monitored these birds (see Chapter 4: Release and Monitoring of Captive-reared

Palila). Wild palila translocated in 2006 and those released from captivity in 2009 were not included in this study.

We either glued or used a figure-8 harness to attach Holohil Systems Ltd. model BD-2 transmitters to palila (Fancy *et al*. 1993; Dougill *et al*. 2000; see Chapter 2: Translocating Wild Palila). The transmitter's battery life was 8–10 weeks, although many birds dropped their transmitters before the battery expired. We tracked birds using Telonics® TR-4 receivers and H-style rubber and metal antennas. To identify locations of daytime activity, we visually located birds at greater than one-hour intervals and marked location coordinates with GPS (global positioning system) units. We also located roosting birds within two hours after sunset in 1997–2004 (hereafter night or nighttime locations or roosts). Additionally, in 2005 we used Telonics® TR-5 receivers and fixed site antenna systems to monitor daily occurrence patterns.

We treated daytime and nighttime locations for individual birds separately. When a translocated bird returned to the western slope, observations from the northern and western slopes were treated separately. To account for possible bias due to autocorrelation among observations, we calculated t2/r2 statistics for a range of minimum times between observations (Swihart and Slade 1985, 1986). We determined that a minimum separation of one day was needed to achieve pseudo-independence of the observations, such that a bird's location on the slope was not strongly dependent on its location the prior day. However, because of the palila's low mobility (see below, and Chapter 2: Translocating Wild Palila) locations on subsequent days were not truly random throughout the region. We excluded data points that were taken within one day of a prior observation.

We used the Minimum Convex Polygon (MCP) bootstrap sample size program (using 100 samples) with the data from the individual bird with the largest number of observations to determine the minimum sample size needed to calculate an accurate home range (Hooge and Eichenlaub 1997). Individuals with fewer than 10 pseudo-independent observations were excluded from further analysis. We used the animal movement extension (Hooge and Eichenlaub 1997) for Arcview GIS 3.2 (ESRI 1999) to calculate 50% and 95% kernel home ranges. Least squares cross-validation (LSCV) was used on each set of observations to determine the individual smoothing parameter (H; Seaman and Powell 1996, Seaman *et al*. 1999). To standardize home range area for comparisons, we re-calculated all home ranges using the median of the smoothing parameters generated for individual kernel home ranges. We used the 50% kernel area for all home range comparisons.

We calculated the distance between the mean centers of day and evening activity for individuals with at least one nighttime roosting and one daytime pseudo-independent observation. We plotted the centers of the nighttime roost and daytime locations on a vegetation class map of the western slope of Mauna Kea (Jacobi 1989) to determine the habitat utilization for each bird.

We grouped birds into non-exclusive subsets for comparisons of home range size and habitat use: breeding adults, non-breeding adults, hatch-year, translocated, non-translocated, males, females, and captive-reared birds. Control birds that remained on the western slope were classified as non-translocated (see Chapter 2: Translocating Wild Palila). No translocated bird that returned from the northern to the western slope met our minimum required observations for home range calculations, but they were still included in the appropriate subset (i.e., non-breeding adults or hatch-year). Many birds fit into multiple subsets (e.g., a non-breeding adult could also be a non-translocated bird). We used Wilcoxon and Kruskal-Wallis non-parametric rank-sum tests to compare home range areas among selected groups and to test for differences in the distance between daytime and nighttime activity. We compared habitat use of daytime and evening activity with a χ^2 test of homogeneity.

Results

The MCP bootstrap sample size test showed a minimum of 20 observations per individual was needed for accurate home range estimation, but only 42 individual birds had sufficient observations. For the purpose of this analysis we decided to use subsets with a minimum of 10 observations for kernel estimates of area with the caveat that area estimates will be biased downward. This condition eliminated all birds from the eastern slope of Mauna Kea. With these relaxed sample size restrictions, we were able to generate kernel home range estimates on 108 birds from 1999–2005 (Figure 12.1). The seven surviving captive-reared birds from the 2003 release were more intensively tracked than other birds (see Chapter 4: Release and Monitoring of Captive-reared Palila) with a minimum of 40 observations each. For purposes of comparison only the first 22 (the mean number of observations from wild birds) pseudo-independent observations were used. Using all the observations from the 2003 captive-reared birds produced consistently and significantly larger home ranges, 12.9 ha for all observations compared to 9.3 ha when limited to the first 22 observations (two-sided paired t-test, $t_6 = 2.444$, $P = 0.0502$). There were not enough observations of the 2004 release captive-reared birds to calculate their home ranges.

Home range size of non-translocated birds on the western slope did not vary significantly among the years 1999–2003 (Kruskal-Wallis $\chi_4^2 = 5.55$, $P = 0.235$). We did not obtain enough locations of non-translocated birds in the other years to calculate accurate home ranges. There also was no significant difference in the home ranges among the birds translocated to the northern slope during 1997–2003 (Kruskal-Wallis $\chi_4^2 = 4.07$, $P = 0.131$). We were unable to calculate kernel estimates of home range for palila in T4 due to an insufficient number (<10) of observations per bird. Home range estimates of birds translocated in 2005 were significantly smaller than for previous translocations (Kruskal-Wallis $\chi_4^2 = 23.5$, $P < 0.001$; Bonferroni corrected multiple Wilcoxon tests $P < 0.01$). More specifically, palila translocated in 2005 used significantly smaller home ranges (Wilcoxon test Z = -5.02, $P < 0.0001$) when compared to the average for each previous translocation. We used Wilcoxon tests and did not find differences in the home ranges of translocated vs. non-translocated birds ($W_{38,20} = 687$, $P = 0.115$), translocated vs. captive ($W_{38,7} = 161$, $P = 1$), or hatch-year vs. adults (Wilcoxon approximate Z = 0.204, $P = 0.839$).

We used data from 79 different birds to measure the distance between the center of daytime and nighttime locations (Table 12.1). Night roost data were not collected in 2005. We detected no significant differences in the distance traveled between daytime and nighttime locations between translocated vs. non-translocated birds (Wilcoxon approximate Z = -1.607, $P = 0.108$), males vs. females (Z = -0.380, $P = 0.704$), hatch-year vs. older birds (Z = 0.412, $P = 0.681$), nor breeding vs. non-breeding adults (Wilcoxon $W_{165,15} = 165$, $P = 0.194$). No significant differences were found when we compared the distance between daytime and nighttime centers of activity between the captive-reared and translocated birds on the northern slope and non-translocated birds on the western slope (Wilcoxon approximate Z = -2.386, $P = 0.017$). The habitat types of daytime locations and nighttime roosts on the western slope differed

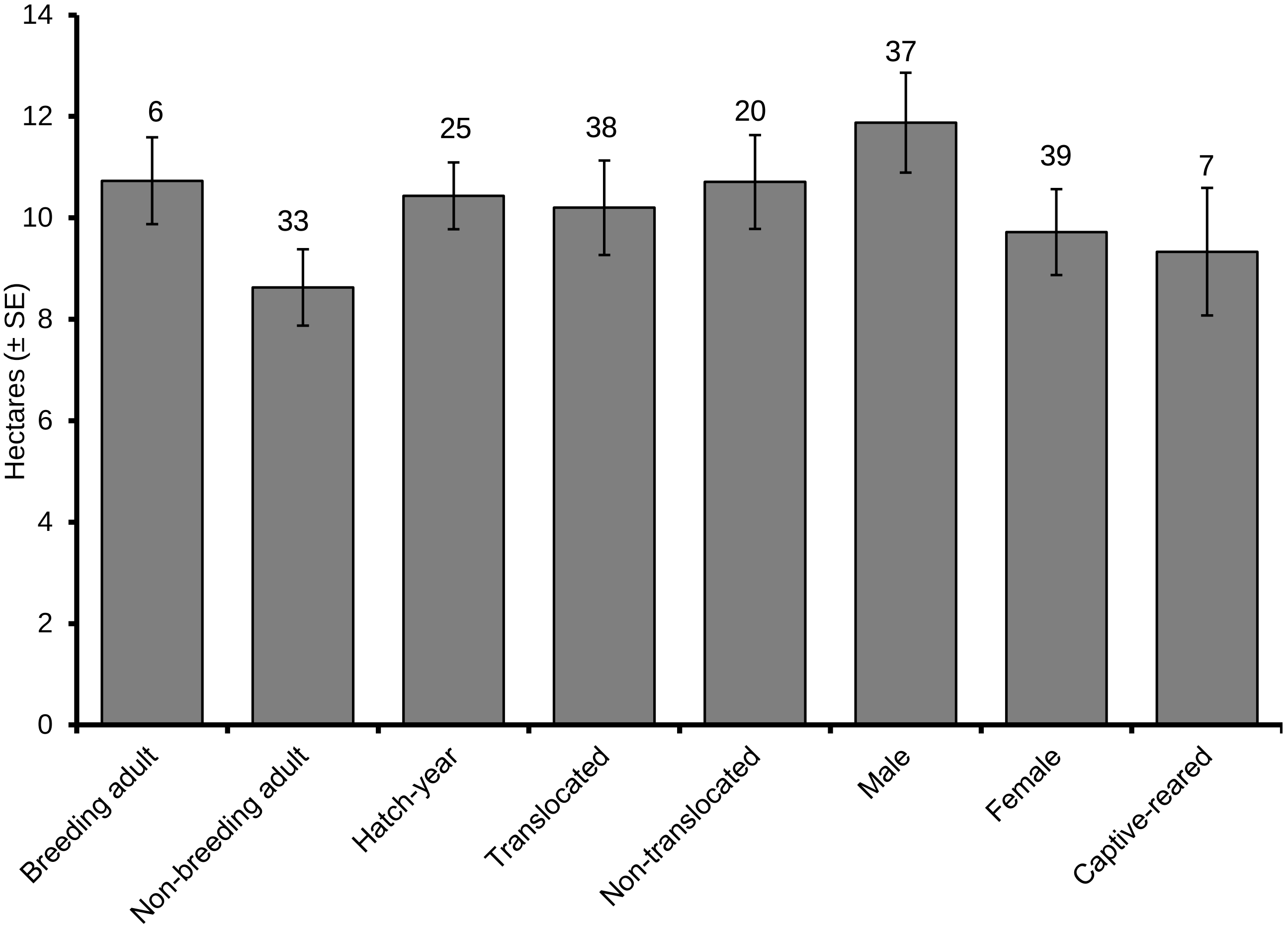

Figure 12.1. Kernel home range estimates (50% probability; ± standard error) for daytime activity of palila on Mauna Kea, Hawai'i, 1999–2005. Number of birds shown above columns.

Table 12.1. Distances (km) between the centers of nighttime roost and daytime locations for palila on Mauna Kea, Hawai'i, 1997–2004.

Subsets	Maximum	Minimum	Mean	*n*
Breeding adult	1.865	0.004	0.480	15
Non-breeding adult	4.986	0.044	0.972	19
Hatch-year	1.673	0.028	0.530	23
Translocated	1.101	0.058	0.340	15
Non-translocated	2.072	0.044	0.798	13
Male	1.865	0.044	0.485	41
Female	3.986	0.044	0.765	37
Captive-reared	0.851	0.161	0.402	7

(Table 12.2; χ^2_6 = 10.49, P = 0.063). A higher proportion of nighttime location centers were in mixed māmane-naio woodland than in māmane woodland.

Table 12.2. Habitat types at the center of day and night roost locations for palila on the western slope of Mauna Kea, Hawai'i, 1997–2002.

Habitat type	Day (n = 116)	Night (n = 55)
Māmane woodland	62	25
Mixed māmane-naio woodland	27	24
Pūkiawe shrub land	18	6
Pasture	1	0
Mixed shrub land	3	0
Bare	5	0

We discovered that palila are much more mobile than previously known. We detected a female second-year palila from T4 moving from the northern slope to the western slope and then returning to the northern slope ("commuting" between slopes). Following the translocation of 62 palila with radio transmitters during March–April 2005 (T5), we documented at least nine palila commuting between the northern (N) and western (W) slopes. The 2005 commuting birds were four males (all after-second-year) and five females (four second-year and one after-second-year), which are the approximate proportion of the age-sex classes of birds moved to the northern slope (see Chapter 2: Translocating Wild Palila). Four of the commuters moved N-W-N, four moved N-W-N-W, and one moved N-W-N-W-N. It is possible that an additional four birds also commuted but the data are inconclusive due to potential errors with radio telemetry signal interpretation. The distance from western slope mist-net stations to the northern release site was 15–16 km. We also detected an unbanded bird on the northern slope from the end of March until the middle of May 2005. Additionally, a banded female palila was observed on the northern slope during July and August 2005, but had not been seen in several months. It is likely that she was translocated in 2004 and had returned for the 2005 breeding season, but her identity is uncertain due to a missing leg band. She nested and fledged one chick.

Palila also exhibited much greater movement within a region (i.e., slope) than was previously known. On the northern slope, at least 18 palila used two distinct patches of māmane habitat that were separated by about three kilometers of shrub habitat (see Introduction for locations on the northern slope). Eight palila were tracked moving only once from the large patch to the smaller patch, five others moved twice (back-and-forth) between patches, four birds moved three times, and one bird moved four times.

Discussion

Habitat availability is one of the most important and relevant issues for palila conservation. How palila use habitat on the western slope of Mauna Kea is key to understanding how to manage the forest for them now and how to plan for improving their habitat in the future. Home range analyses provide valuable information that, when used in combination with habitat use and food availability, can greatly aid in planning translocations and releases of captive-reared birds. For example, while we found no significant differences between the home range sizes of translocated and non-translocated birds, translocated birds' daily movements were smaller than non-translocated birds. This suggests that there are distinct differences between habitats on the northern and western slopes of Mauna Kea that influence palila habitat use. Mature māmane stands and mixed māmane-naio woodlands are less abundant at the release site. The absence of larger stands of these forest types could influence the persistence time of translocated palila on the northern slope.

Palila night-roosting behavior was unknown before we began our research in 1998. We determined that the habitat selected for nighttime roost sites differed from that of daytime use areas. Mixed māmane-naio woodlands are important to palila for night roosting, possibly because the denser canopy cover provides thermoregulatory benefits and protection against aerial predators. Maintaining sufficient night roosting cover could have important implications for managing palila habitat.

Previously, palila were not known to move far around Mauna Kea (Banko *et al.* 2002). We observed that translocated palila travelled between the northern and western slopes. The distance from the capture sites to the release site was 15–16 km. Nevertheless, radio-tagged, commuting palila were not detected between the two slopes, suggesting that palila moved rapidly and without using the habitat between the slopes. Thus, restoring habitat between the two slopes might encourage the movement of palila and connectivity of populations around the mountain. We also found that palila translocated to the northern slope used two distinct patches of māmane habitat that were separated by about 3 km of shrub habitat. This finding could be helpful in developing habitat restoration strategies. For example, focusing limited resources on restoring patches of habitat might allow palila to persist among multiple sites until habitat can be restored across the wider landscape.

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13 HABITAT USE AND FORAGING PATTERNS

Steven C. Hess, Paul C. Banko, Linda J. Miller, Leona P. Laniawe

Introduction

Hawaiian bird communities have suffered greater losses of species in dry forests than in moist forests (W. Banko and P. Banko 2009), as have birds in other tropical regions (Stotz *et al.* 1996). The endangered finch (Fringillidae: Drepanidinae), palila (*Loxioides bailleui*), found only in subalpine woodland of Mauna Kea Volcano on the island of Hawaiʻi, is now the only remaining endemic bird that requires dry forest (Scott *et al.* 1986, Banko *et al.* 2009). Many species of Hawaiian finches, now extinct, depended heavily on the seeds of single species of trees for food (Perkins 1903, P. Banko and W. Banko 2009). Palila were reported to eat caterpillars, other insects, and the fruit of naio (*Myoporum sandwicense*), but seeds and flowers of the leguminous māmane (*Sophora chrysophylla*) tree were found to be the most important component of their diet (Perkins 1903, Banko *et al.* 2002a). Palila move in response to māmane seedpod (pod) availability (Hess *et al.* 2001), but when māmane resources are scarce they consume alternate plant resources, such as the fruits of naio (Banko *et al.* 2002a).

Subalpine woodland habitat has been reduced and degraded by browsing feral mammals since the arrival of Europeans in Hawaiʻi (Warner 1960, Scowcroft and Giffin 1983, Hess and Banko 2011). Palila were more widely distributed in dry forests on the islands of Hawaiʻi, Oʻahu, and perhaps other islands before human contact (Wilson and Evans 1890−1899; Rothschild 1893−1900; Perkins 1893; Munro 1944; Berger 1972; van Riper 1978, 1980a; Olson and James 1982). Today, the palila inhabits an area on the western slope of Mauna Kea that is about five percent of their historical distribution (Scott *et al.* 1984, 1986; Jacobi *et al.* 1996; Banko *et al.* 1998; Gray *et al.* 1999; Leonard *et al.* 2008; Banko *et al.* 2013).

As populations of feral mammals have been culled, beginning in 1980, māmane regeneration has increased (Scowcroft and Conrad 1988, Hess *et al.* 1999, Reddy *et al.* 2012). In addition, decreased browsing has allowed many trees to regrow their lower branches, thus providing greater foraging opportunities for birds (Banko *et al.* 2013). Nevertheless, palila have not recovered in much of their former range, despite somewhat improved habitat conditions around Mauna Kea.

Recovery has been delayed partly because palila seldom forage or nest in saplings and small trees (Banko *et al.* 2002a) and many years are required before recently recruited trees are large enough to benefit the birds (Scowcroft and Conrad 1988). In addition, site tenacity (Fancy *et al.* 1993; see Chapter 12: Habitat Use, Home Range, and Movements), predation (Amarasekare 1993, 1994), or limited food availability due to severe, long-term habitat degradation (Scott *et al.* 1984, Jacobi *et al.* 1996, Fancy *et al.* 1997, Pratt *et al.* 1997, Banko *et al.* 2009) may still prevent palila from recolonizing parts of their former range. The availability of māmane pods and alternate food resources may not be sufficient to sustain palila recovery throughout most of these areas, especially during drought, which has been prevalent and severe since 2000 (Banko *et al.* 2013). Palila habitat is also threatened with alteration and destruction due to the invasion of alien grasses which have added continuous fine fuels, thus increasing the likelihood of intense fires (Smith and Tunison 1992, Banko *et al.* 2009, Thaxton and Jacobi 2009) and altered vegetation structure in the long-term (D'Antonio *et al.* 2011).

We investigated palila foraging behavior and food selection in two woodland types where food resource availability differed (Hess *et al.* 1999, 2001) to determine the degree of dependency on māmane resources and the importance of alternate foods. High-elevation woodland provides the highest availability of māmane flowers and pods, but there are few alternate food resources. Mixed naio-māmane woodland, at lower elevation, contains fewer māmane resources but abundant naio fruits. The objectives of this study were to determine if: 1) palila foraged more in māmane than in naio where the two tree species co-dominate; 2) naio fruits or māmane flowers are important alternate food resources in areas of low māmane pod availability; and 3) palila spend more foraging time on māmane seeds than flowers where they consume more flowers than seeds. These results can be used to evaluate the relative importance of alternate food resources and māmane availability for habitat restoration and palila recovery.

Methods

Study Area

Four study sites, each with five transects, were arranged on an elevation gradient extending from 1,978 to 2,816 m in leeward, dry, subalpine woodland in the Mauna Kea Forest Reserve, island of Hawaiʻi (19°50'N, 155°35'W). The sites were designated, in order of descending elevation (see Introduction): PL Mauka (11.8 ha, 2,591−2,804 m), PL Makai (10.5 ha, 2,286–2,591 m), Manao (17.8 ha, 2,286–2,530 m), and Ahumoa (20.3 ha, 2,073–2,243 m). The PL Mauka and PL Makai sites above 2,317 m were dominated exclusively by māmane with 5−30% canopy cover; while the Manao and Ahumoa sites below 2,437 m contained a high proportion of co-dominant naio with as much as 60% overall canopy cover. Overall canopy cover averaged 30%, and canopy height was generally short (3−8 m). Vegetation structure was described by Hartt and Neal (1940), van Riper (1980b), Scowcroft and Giffin (1983), and Hess *et al.* (1999), and tree phenology was described by van Riper (1980b) and Banko *et al.* (2002b).

Substrates were severely drained vitrandepts composed of volcanic cinder and ash with exposed basaltic lava flows. Surface substrate age ranged between 4,000 and 14,000 years (Wolfe and Morris 1996). Most of the organic soil layer was lost to erosion and grazing since Western colonization (Warner 1960). Temperature averaged 11.1 ± 1.5°C annually and rainfall averaged 511 mm (Juvik *et al.* 1993, Juvik and Nullet 1993). Long-term rainfall data from 1940 through 1977 indicate that the wettest months are November−May with average rainfall >40 mm/month. June is the driest month and rainfall averages <40 mm/month during June−October (Banko *et al.* 2013). In addition to rainfall, there is substantial fog-drip interception by trees from a cyclic diurnal influx of humid low-elevation air which may account for as much as 38% additional precipitation (Juvik and Nullet 1993).

Subalpine woodlands are cooler than lowland subtropical dry forests (Murphy and Lugo 1986) with frequent freezing temperatures. Rain shadow effects of Mauna Kea and extreme substrate drainage account for the semi-arid aspect of the woodland. Māmane woodlands developed in the absence of herbivorous mammals, as did all other Hawaiian forests (Carlquist 1970). As numbers of browsing ungulates have been culled in the subalpine woodland of Mauna Kea, alien grasses, such as *Dactylis glomerata*, *Holcus lanatus*, *Anthoxanthum odoratum*, and *Poa pratensis*, have become the dominant understory vegetation in some areas and have the potential to affect ecosystem processes such as the natural fire regime and māmane regeneration (Smith and Tunison 1992, Amarasekare 1993, Williams 1994, Hess *et al.* 1999, Thaxton and Jacobi 2009).

Tree Density

We sampled five transects from each of the four sites using the point-centered quarter method to estimate mature tree density (Mueller-Dombois and Ellenberg 1974, Hess *et al.* 1999). Transect length varied from 900–1,200 m. In each study area, we randomly selected 20 point-centers along two transects and 10 point-centers along three transects. We selected the nearest mature tree of crown size equal or greater than 2 m height and width within each quarter. We measured the distance from each selected tree crown center to the sample point to ±0.5 m. We considered all conspecific stems emerging from the ground within one-meter radius of the selected individual to be from the same individual. We also measured elevation at each point-center.

We calculated tree density for each transect with Pollard's (1971) formula for an unbiased population density estimate of the point-centered quarter method where N_P = the population density estimate, n = the number of random points, and r_{ij} = the distance from the random point i to the nearest organism in quadrant j.

$$N_P = 4(4n\text{-}1)/\pi\,\Sigma\,(r_{ij}^2) \qquad \text{(Equation 1)}$$

We estimated the density of naio directly in the PL Mauka and PL Makai study sites because this species was too rare for adequate sampling by transects. We located all naio trees within the PL Mauka and PL Makai study sites. The number of naio trees was divided by the area of the study site to calculate density. Error estimates could not be determined by this method. Māmane density estimates were log transformed and analyzed with the GLM procedure (SAS Institute 1985).

Phenology

Each month from June 1994 until December 1995, we counted the number of expanded green pods (≥3 mm across the widest dimension of one or more enclosed seeds) and the number of open flowers on the nearest māmane tree (≥2 m tall) located at 150-m intervals along the same transects where we estimated mature tree density. We multiplied the transect pod and flower means by the estimate of tree density at each transect to estimate availability of flowers and pods per hectare. We log transformed both independent variables and analyzed them with the GLM procedure (SAS Institute 1985) to test for differences among study sites and assessment periods. The availability of naio fruits was not included in the analysis because it was superabundant (>50% of trees bore fruit on >25% of their branch tips each month [Banko *et al.* 2002b]) during the entire study in the two sites where naio was co-dominant.

Behavioral Observations

We observed the behavior of palila, some of which were marked with unique combinations of three colored leg bands and a numbered U.S. Fish and Wildlife Service aluminum band (see Jeffery *et al.* 1993, Lindsey *et al.* 1995), during June 1994–November 1995 to quantify time birds spent in foraging and other activities. We recorded the study site, location, date, time, age, and sex for every palila that we observed during semi-systematic sweeps of the four study sites. Because palila density differed among the four study sites (Hess *et al.* 2001), we did not obtain equal numbers of behavioral observations for each study site. We continuously recorded the use of plant species, movements, food items, self-maintenance, and social interactions during indeterminate length observations of palila activity. For analysis, we truncated the first 10 seconds of each observation to reduce discovery bias (Bradley 1985), and truncated each observation to 100 seconds in total length to standardize the probability of rare events (Morrison 1984, Hejl *et al.* 1990). To reduce autocorrelation, sequential observations of the same individual (banded) within the same day or unidentified individuals (unbanded) at the same location within the same hour were not included in this analysis (Hejl *et al.* 1990). We analyzed 990 observations which met these criteria: 416 observations from PL Mauka; 180 from PL Makai; 237 from Manao; and 157 from Ahumoa. We compared the proportion of time palila spent in māmane to the proportional availability of māmane in each study area. We also compared the number of food items used by palila per 100-second observation to the handling time of food items in each study area.

Results

Tree Density

Māmane densities differed significantly among study sites (ANOVA, df = 3, $P < 0.005$) but were highest at PL Mauka (df = 1, $P < 0.0001$; Figure 13.1). Māmane densities in the māmane-dominated PL Mauka and PL Makai sites were higher (df = 1, $P < 0.0001$) than in mixed naio-māmane woodland in the Ahumoa and Manao sites. Naio was rare in the māmane woodland sites but was more abundant than māmane in the mixed woodland sites (t-test, df = 9, $P < 0.03$). At PL Mauka and PL Makai, we found 1 and 11 naio trees and calculated densities of 0.085 and 1.052 naio/ha, respectively, while densities in the Manao and Ahumoa sites were 60.9 and 212.5 naio/ha, respectively.

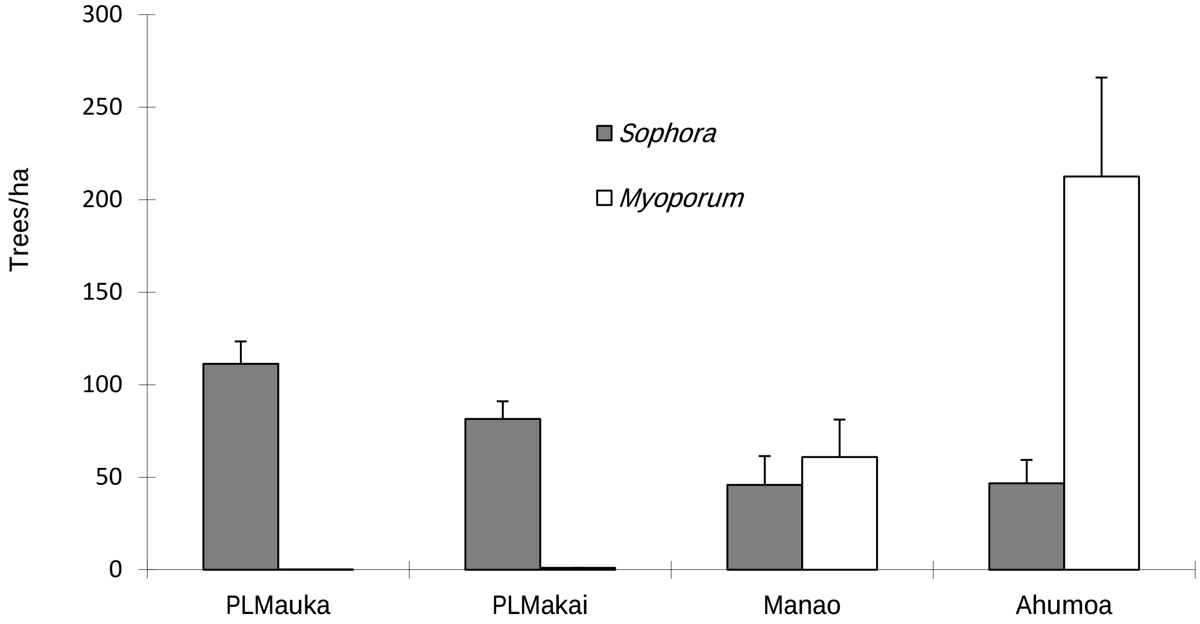

Figure 13.1. Density (trees/ha + SE) of *Sophora chrysophylla* (māmane) and *Myoporum sandwicense* (naio) trees (≥2 m tall) at four study sites (PL Mauka, PL Makai, Manao, Ahumoa) on the western slope of Mauna Kea, Hawaiʻi. *Myoporum sandwicense* density was measured by locating all individuals at PL Mauka and PL Makai study sites. Other density estimates were based on transect sampling.

Habitat Use

We calculated the proportional availability of māmane and naio trees at each study site and compared the proportion of time palila (all age and sex categories combined) spent in each species (Figure 13.2). In the PL Mauka and PL Makai sites, where naio availability was extremely low, palila were in māmane trees >95% of the time. They spent <3% of the time in naio, and the remainder was spent in grasses as well as *Verbascum thapsus* and *Chenopodium oahuense*. In the Manao and Ahumoa sites, where the availability of naio trees was 1.3 and 4.6 times greater than that of māmane trees (Figure 13.1), palila spent 1.7 and 3.9 times more time in māmane than in naio (Figure 13.2). We did not test the statistical significance of these results (Cherry 1998), because māmane was so disproportionately utilized.

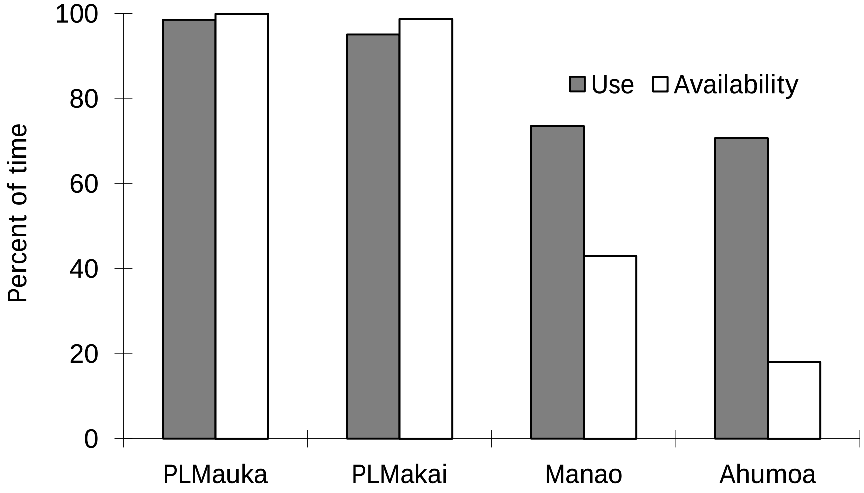

Figure 13.2. Proportion of time palila were observed in māmane (use) in comparison to its availability at four study sites (PL Mauka, PL Makai, Manao, Ahumoa) on the western slope of Mauna Kea, Hawaiʻi.

Māmane Phenology

Māmane flower availability differed among study sites (ANOCOVA, df = 3, $P < 0.0001$; Figure 13.3). Flowers were more abundant at PL Mauka than they were at the other sites (df = 1, $P < 0.0001$) and flowers were more abundant at the two māmane woodland study sites than they were at the naio-māmane woodland sites (df = 1, $P < 0.0001$). Pod availability also differed among study sites (df = 3, $P < 0.0001$; Figure 13.3), being highest in PL Mauka (df = 1, $P < 0.0001$). Pods were more abundant in the māmane woodland study sites than they were in the mixed naio-māmane study sites (df = 1, $P < 0.0001$). Pod abundance in the Ahumoa study site was higher than was flower abundance (Figure 13.3) because pods occurred in the greatest abundance at the beginning of the study and the preceding flowering episode was not represented in the data.

Foraging Behavior

Palila spent 40% of their daily time in foraging and food consumption. Palila sever individual māmane pods with their mandibles then carry the pod in their bills until they find a suitable

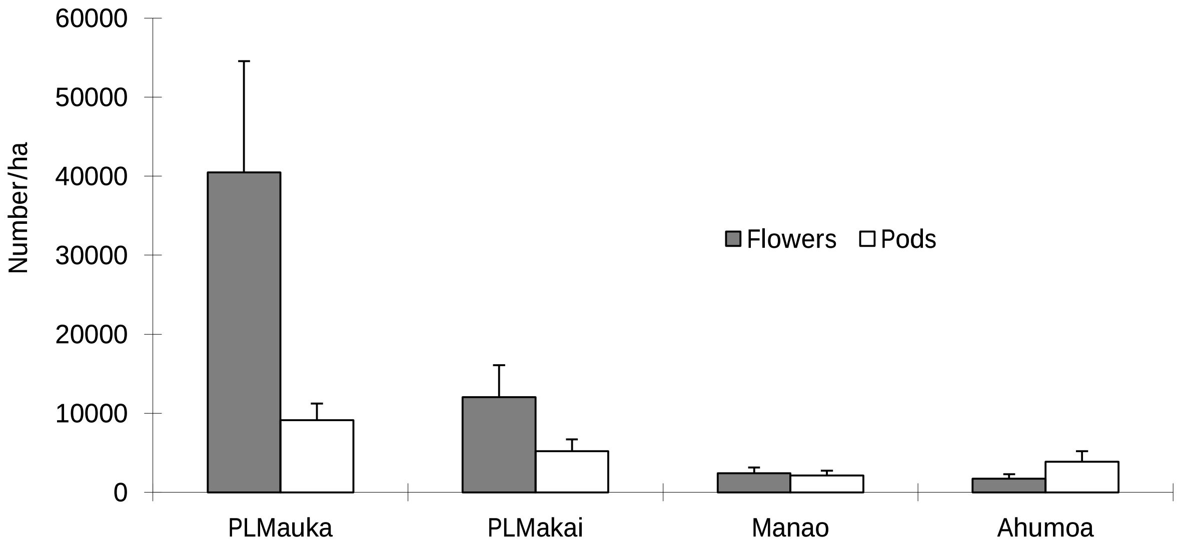

Figure 13.3. Average number (+ SE) of *Sophora chrysophylla* (māmane) flowers and pods available per hectare (ha) at four study sites (PL Mauka, PL Makai, Manao, Ahumoa) on the western slope of Mauna Kea, Hawai'i.

perch. They grasp the pod with their feet and pull and twist sharply with their head and neck to tear off pieces of the tough outer covering of the pod to expose the tender green seeds. They consume the green cotyledons and germ of the seed but leave behind the seed coat within the discarded pod (Banko *et al.* 2002a, c). Palila rarely eat the ripening yellow- or orange-coated seeds and probably cannot eat fully ripened seeds due to their extreme hardness. Palila harvest ripe (white) naio fruit in a similar manner. They pluck an individual fruit from its stem, usually carry the fruit in their bill to a suitable perch, grasp the fruit with one foot, and eat the outer soft pulp but not the large hard seed inside.

Palila sever māmane flowers with their mandibles and consume the reproductive parts. Anthers are frequently found in fecal samples (Banko *et al.* 2002a; see Chapter 14: Diet). They also hold severed māmane flowers with one foot and bite through the calyx to obtain nectar. Palila eat flower buds, immature pods, and developing foliage of māmane. They have been observed eating the fruit, seed, flower, foliage, or meristem of 14 plant species in 12 families (Table 13.1).

Food Selection

Palila obtained 90% of their food items from māmane and naio and spent 93% of their foraging time in these two tree species. The remainder of their diet was comprised of (in order of importance; Table 13.1) leaves of māmane, naio, and *Chenopodium oahuense*; *Verbascum thapsus* flowers; grass seeds; *Solanum americanum* leaves; *Coprosma montana* and *Santalanum paniculatum* fruit; and other small, unidentified items, possibly fungi or arthropods, in lichen or between bark fissures on tree trunks. We made no definitive observations of palila eating arthropods during this study, although we observed foraging maneuvers consistent with insectivory. Palila consume the larvae of *Cydia* (presumably *C. plicata* [Oboyski 2011]: Tortricidae) moths, which they find inside māmane pods (Banko *et al.* 2002a; see Chapter 14:

Table 13.1. Plant species parts observed being eaten by palila during systematic and incidental observations on Mauna Kea, Hawai‘i. Species are ranked by the number of observations of each food item (not shown). Species are native unless otherwise noted. Observations from the western slope (West; *n* = 990) were collected during systematic foraging surveys while data from other slopes (East, North) were collected incidentally.

Species	Family	Parts	Slope
Sophora chrysophylla	Fabaceae	seeds, flowers, leaves, immature pods	West
Myoporum sandwicense	Myoporaceae	fruit, leaves	West
Chenopodium oahuense	Chenopodiaceae	leaves	West
Stenogyne microphylla	Lamiaceae	fruit, leaves	West
Dactylis glomerata[1]	Poaceae	seeds	West
Verbascum thapsus[1]	Scrophulariaceae	flowers	West
Santalanum paniculatum	Santanalaceae	fruit, flowers, leaves[2]	West
Rumex acetosella[1]	Polygonaceae	leaves	West
Coprosma montana	Rubiaceae	green stems, fruit	North
Solanum americanum	Solanaceae	leaves	West
Physalis peruviana[1]	Solanaceae	fruit	North
Rubus hawaiiensis	Rosaceae	fruit	North
Osteomeles anthyllidifolia	Rosaceae	fruit	East
Dubautia arborea	Asteraceae	leaves	East

[1] Introduced species

[2] Palila were noted eating *Santalanum* leaves on eastern and northern slopes of Mauna Kea during incidental foraging observations.

Diet). In this study, we could not determine whether palila ate caterpillars or only seeds when they opened a pod.

Palila consumed more māmane seeds than flowers in māmane woodland, while they consumed more māmane flowers than seeds in mixed woodland (Figure 13.4). In all areas combined, palila spent more time consuming māmane seeds than flowers (Figure 13.5). Naio fruits composed <11% of the food items consumed by palila, and the birds spent <10% of their foraging time in this tree species at the Manao and Ahumoa study sites.

Discussion

Our results demonstrated strong preference for māmane, with palila spending proportionally more time in māmane trees and using māmane foods in much greater proportion to their availability than other foods. In mixed naio-māmane woodland, where naio density was greater than māmane density, palila spent more than twice as much time in māmane trees. Palila densities were related to pod availability and were higher in māmane woodland than in mixed woodland where māmane density was lower (Hess *et al.* 2001). Palila demonstrated limited ability to exploit alternate food resources, using naio fruits only occasionally and apparently only when the availability of māmane was reduced (Hess *et al.* 2001).

Although palila consumed more flowers than pods in mixed woodland, they spent more time foraging on pods than other food items in both woodland types. Palila consumed reproductive parts and foliage of māmane, but took a higher proportion of māmane pods than other māmane food items relative to their availability. The importance of māmane seeds in relation to

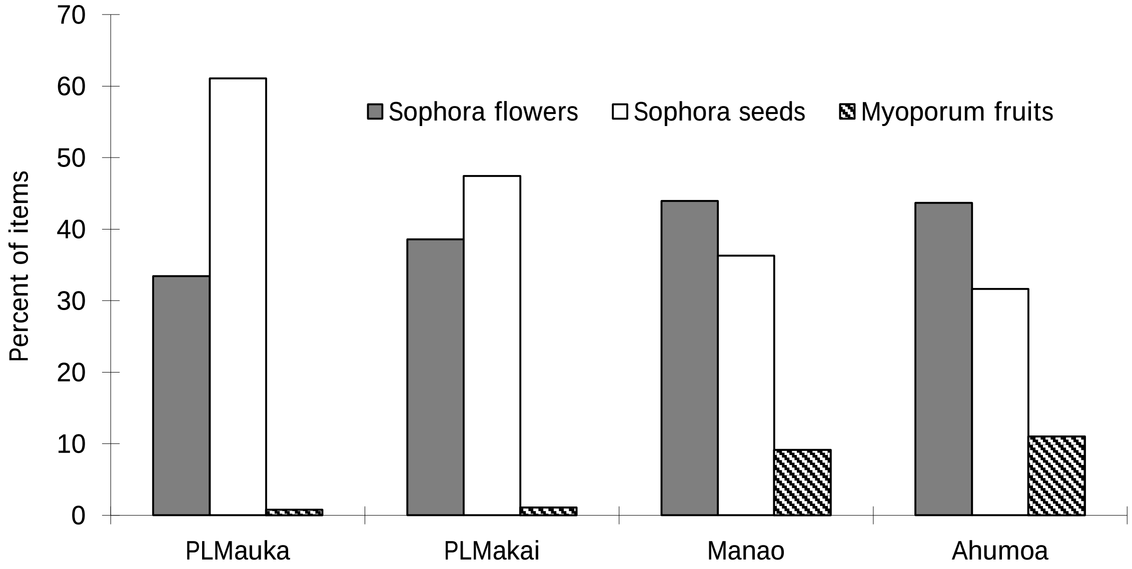

Figure 13.4. Proportion (percent) of food items (māmane [*Sophora*] flowers and seeds and naio [*Myoporum*] fruits) consumed by palila at four study sites (PL Mauka, PL Makai, Manao, Ahumoa) on the western slope of Mauna Kea, Hawai‘i.

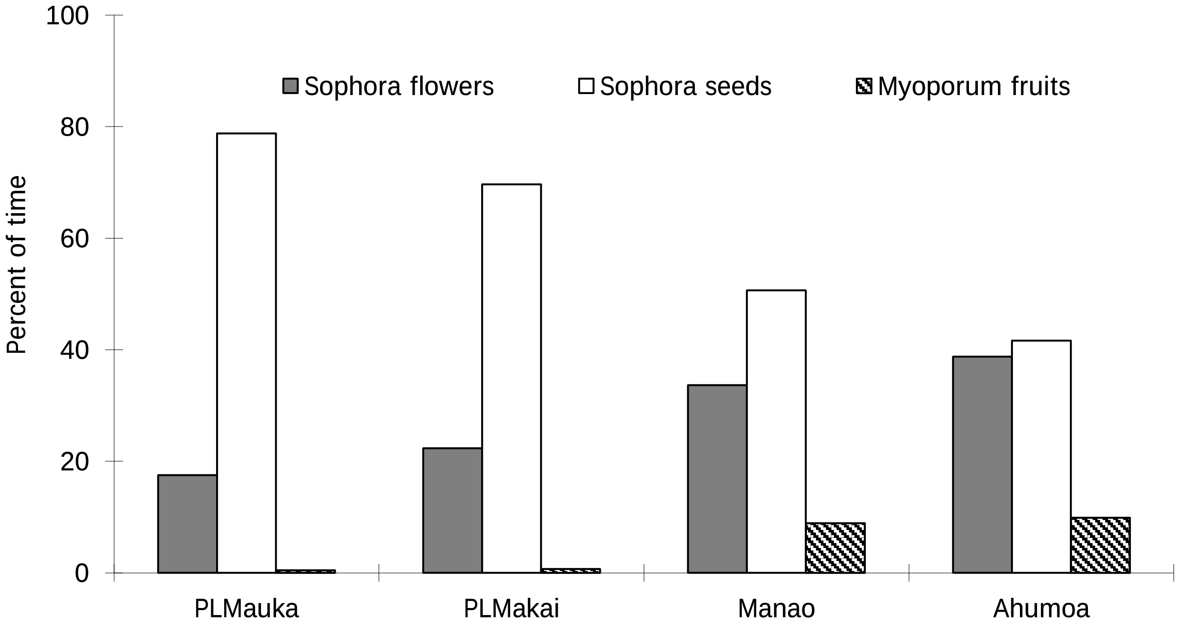

Figure 13.5. Percentage of time palila spent consuming food items (māmane [*Sophora*] flowers and seeds and naio [*Myoporum*] fruits) at four study sites (PL Mauka, PL Makai, Manao, Ahumoa) on the western slope of Mauna Kea, Hawai‘i.

movement, breeding, and survival of palila has been well documented (van Riper 1978, 1980a; Scott *et al.* 1984; Fancy *et al.* 1993; Lindsey *et al.* 1995; Hess *et al*. 2001). The nutritional value of seeds is high (Banko *et al.* 2002c) and contributes the largest proportion of food mass in the diet of palila (Banko *et al.* 2002a; see Chapter 14: Diet). Palila consume flowers and flower buds in the course of searching for pods, but palila densities were not related to flower availability (Hess *et al.* 2001).

This degree of single species dependency on plant foods, primarily seeds, is rare among birds (Newton 1973, Benkman 1993) and illustrates unique adaptations that also occurred in other Hawaiian species that are now extinct (P. Banko and W. Banko 2009). Palila are the last remaining honeycreeper in the main Hawaiian Islands to specialize on seeds and require dry forest habitat. Palila are morphologically and behaviorally adapted to open unripe māmane pods and consume the seeds, possessing a stout bill for tearing open pods while they grasp them with their feet. Captive-reared palila learned to open māmane pods and consume seeds without the guidance of adult birds, but methods for opening pods and extracting seeds varied somewhat from methods used by wild birds (Frayne 2007; see Chapter 4: Release and Monitoring of Captive-reared Palila), demonstrating innate ability to recognize and process pods but also suggesting the benefits of parental teaching (Miller 1998).

Although Perkins (1903) found that stomachs of palila contained a variety of caterpillars, and van Riper (1980a) and Scott *et al.* (1986) reported that palila took caterpillars and other insects, we did not observe palila capturing arthropods from flowers, foliage, or bark during this study. Nevertheless, there have been other observations of palila feeding on caterpillars (Banko *et al.* 2002a). The number of arthropod fragments found in fecal samples collected from adult palila (see Chapter 14: Diet) suggest that substantial insectivory is undetected by behavioral observation. Small arthropods living within or on flowers, foliage, lichen, or bark could easily have been taken undetected during foraging observations. Parts of *Cydia* caterpillars that inhabit māmane pods were also found in a high proportion of feces from nestling palila and in many fecal samples collected from adults (see Chapter 14: Diet). Perkins (1903) reported that palila fed caterpillars to their young, and van Riper (1980a) found that palila took more insects during breeding season.

Palila may have had access to many other species of plants when they were distributed at lower elevation and on other islands. There is very little information on palila diet from outside of their current range. However, sub-fossil data suggest they probably occurred exclusively in dry forests and woodlands dominated by māmane (Olson and James 1982). Palila occur to the tree line (ca. 2900 m) where very few other woody plant species exist and alternative food resources are very scarce. Even at the lower limit of their range (ca. 1800 m), palila make little use of alternative foods. Palila may have consumed fruits of *Coprosma*, *Santalanum*, *Rubus*, and other dry forest trees and shrubs where they were once more common and widely distributed. Second-year palila translocated to the northern slope of Mauna Kea in 1997 consumed fruit and young green stems of *Coprosma* and fruit of *Physalis peruviana* and *Rubus hawaiiensis* (see Chapter 2: Translocating Wild Palila), which were not documented on the western slope probably because of extremely low availability (Hess *et al.* 1999).

Palila reproductive effort and juvenile survivorship are correlated with māmane pod availability (Lindsey *et al.* 1995, Pratt *et al.* 1997). Drought years associated with the southern oscillation result in low pod availability, little nesting activity, and low capture rates of native birds (Lindsey *et al.* 1997). The palila population estimate is characterized by high variability and has declined sharply since 2003 in response to drought (Banko *et al.* 2013).

In areas of mixed woodland where browsing ungulates have been culled, māmane regeneration is much greater than naio, and the woodland community is shifting towards māmane dominance (Hess *et al.* 1999). If māmane density continues to increase in the mixed naio-māmane woodland, palila densities may also increase, although they may ultimately be limited by drought (Banko *et al.* 2013). Restoration and protection of māmane in mixed woodland and other areas, such as the northern and southern slopes of Mauna Kea and areas on the western slope adjacent to the core habitat of the palila population, would increase the overall phenological diversity and the likelihood of birds finding more food patches in years of low food availability (van Riper 1980b, Scott *et al.* 1984, Banko *et al.* 2002b). Habitat restoration would benefit the recovery of the palila and allow this highly specialized Hawaiian honeycreeper to recolonize areas within its former range (Scott *et al.* 1984, 1986; Fancy *et al.* 1993, 1997; Banko *et al.* 2009).

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14 DIET

Peter T. Oboyski, Paul C. Banko, John W. Slotterback

Introduction

The stout beak of the palila (*Loxioides bailleui*) is adapted for extracting and consuming seeds from māmane (*Sophora chrysophylla*) pods, and the palila is one of the most specialized of the Hawaiian honeycreepers (Banko and Banko 2009). All observers have remarked upon the singular importance of māmane seeds in the diet of the palila, and this dependence affects virtually every aspect of the palila's ecology (Banko *et al.* 2009). Nevertheless, Perkins (1903) noted that palila also often consumed caterpillars. Although observations of foraging palila confirm that māmane seeds are the most frequently eaten items, other foods may contribute to the diet without necessarily being recorded by observers (see Chapter 13: Habitat Use and Foraging Patterns). For example, māmane seeds are also the only known host for several species of endemic Hawaiian *Cydia* (Tortricidae) caterpillars (Zimmerman 1978), which are encountered by palila when extracting the seeds from pods. We analyzed palila feces for the presence of these auxiliary food items and report our results relative to bird age, season, and habitat type.

Methods

We established banding stations in two habitat types: māmane-dominant forest (upper elevation) and naio (*Myoporum sandwicense*)-dominant forest (lower elevation; Introduction, Figure I.2). Stations were established in areas of high bird activity to increase banding success. We monitored nests in these same general areas. The palila breeding season generally extends from March to September (Banko *et al*. 2002). Based on the month they were collected, samples were considered to be within (March–September) or outside the breeding season. Samples collected in March and September were considered to be on the margin of the breeding season. Palila feces were collected during 1989–1996 while birds were banded and measured. Fecal samples were also collected from nestling palila during nest monitoring. Feces were immediately placed into vials containing 70% ethyl alcohol and returned to the laboratory for analysis. We recorded the age and sex of the bird (when discernible), location, and date of capture. Fecal samples were dissected under a microscope. Fragments of flowers, grass seeds, *Cydia* caterpillars, and other arthropods were removed and compared with voucher specimens collected from the field. The type and number of each fragment were recorded for each sample. We estimated by eye the proportion of the samples comprised of māmane seeds.

We used Fisher's exact test for all statistical analyses because the data were frequencies of fecal samples containing particular foods. Only presence or absence of each food type was used for analysis because food retention time may differ according to bird age and food type. We compared the frequency of foods among the different age groups (nestlings [N], hatch-year [HY], second-year [SY], after-second-year [ASY]), collection areas (habitat type), and seasons (breeding and non-breeding). We also compared the frequency of *Cydia* fragments in the diets of ASY males and females.

Results

Māmane seeds composed over 90% of fecal matter by volume in 259 samples. Other items in the diet included māmane flower parts (anthers, stamens, and pistils), seed coats of grasses, and fragments of arthropods (legs, pieces of integument, head capsule fragments, and mandibles). The most frequently encountered arthropod fragments were caterpillar mandibles and head capsule fragments of *Cydia* spp. (probably *C. plicata* [Oboyski 2011]). *Cydia* caterpillar fragments were present in a significantly greater proportion of fecal samples of palila nestlings than in HY, SY, or ASY birds (Fisher's exact test: all $P < 0.001$; Figure 14.1). *Cydia* fragments were found significantly less often in SY birds than they were in HY or ASY birds ($P < 0.001$; Figure 14.1). The frequency of *Cydia* fragments in ASY males and ASY females was not significantly different ($P = 0.358$). The frequency of *Cydia* in fecal samples overall did not vary significantly between habitat types ($P = 0.174$, all bird age classes; Figure 14.2) or within each age class between habitat types (N, $P = 0.820$; HY, $P = 0.172$; SY, $P = 0.385$; ASY, $P = 0.162$). The overall frequency of *Cydia* samples was not significantly different between the breeding and non-breeding season ($P = 0.297$, all bird age classes) or within each age class between seasons (HY, $P = 0.888$; SY, $P = 0.656$; ASY, $P = 0.830$; Figure 14.3).

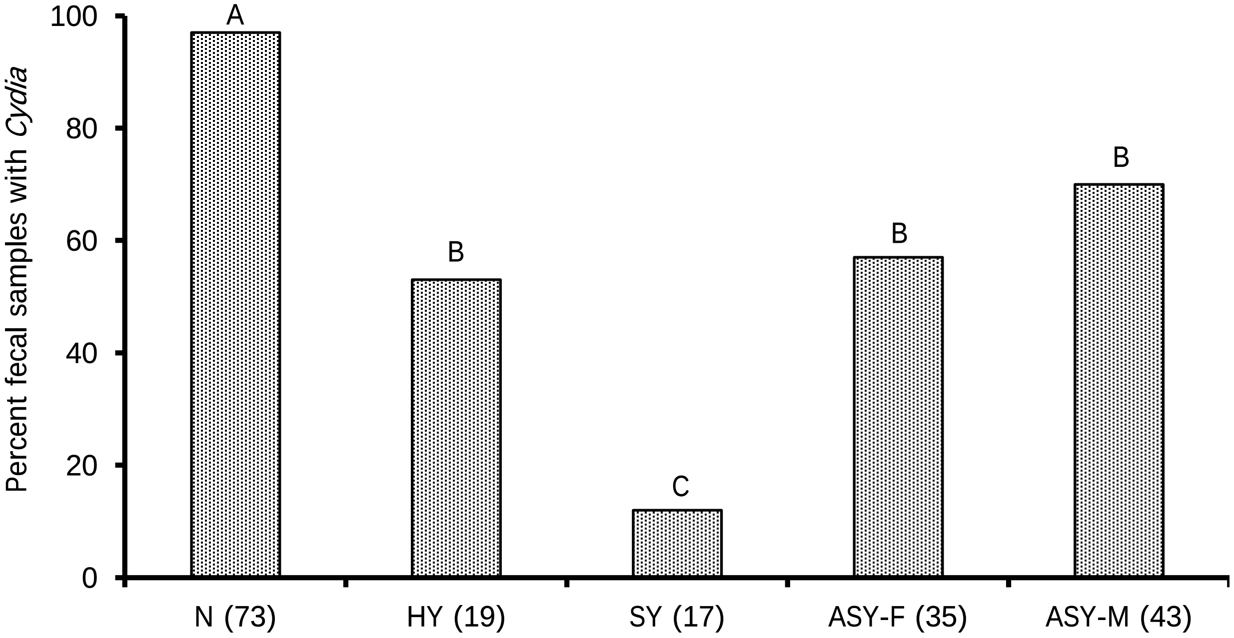

Figure 14.1. Percent of palila fecal samples with *Cydia* present. Sample sizes are shown in parentheses. N = nestling, HY = hatch-year, SY = second-year, ASY-F = after-second-year female, ASY-M = after-second-year male. Different letters above bars indicate significant differences (Fisher's exact test, $P < 0.001$).

Anthers from māmane flowers were readily distinguished in fecal samples. Anthers were most prevalent in samples from nestlings, although this was not significantly greater than in HY samples ($P = 0.136$). A significantly greater proportion of N and HY fecal samples contained anthers than was found in SY or ASY samples (all comparisons $P < 0.05$; Figure 14.4). No significant difference was found in the incidence of anthers in samples from SY and ASY birds ($P = 0.143$). Grass seed coats were easily distinguished in fecal samples. Grass seeds were found significantly more often in N samples than they were in SY or ASY samples ($P = 0.002$

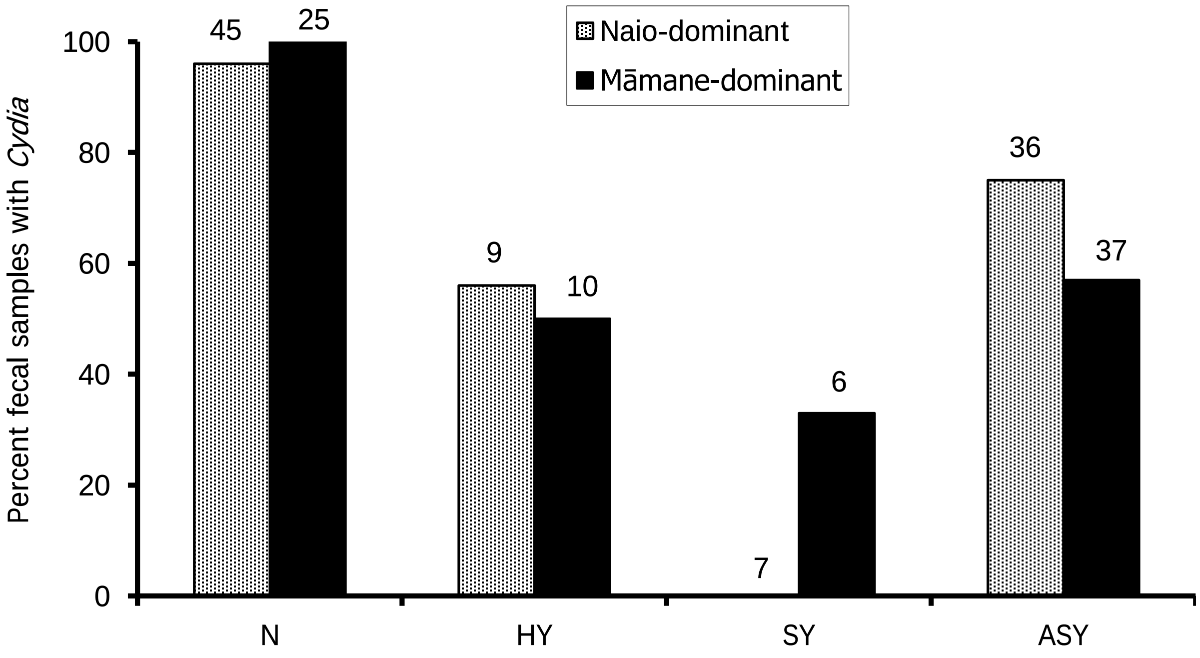

Figure 14.2. Percent of palila fecal samples containing *Cydia* fragments by habitat type. Sample sizes are shown above bars. N = nestling, HY = hatch-year, SY = second-year, ASY = after-second-year. There were no significant differences between pairs of bars (Fisher's exact test, $P > 0.05$).

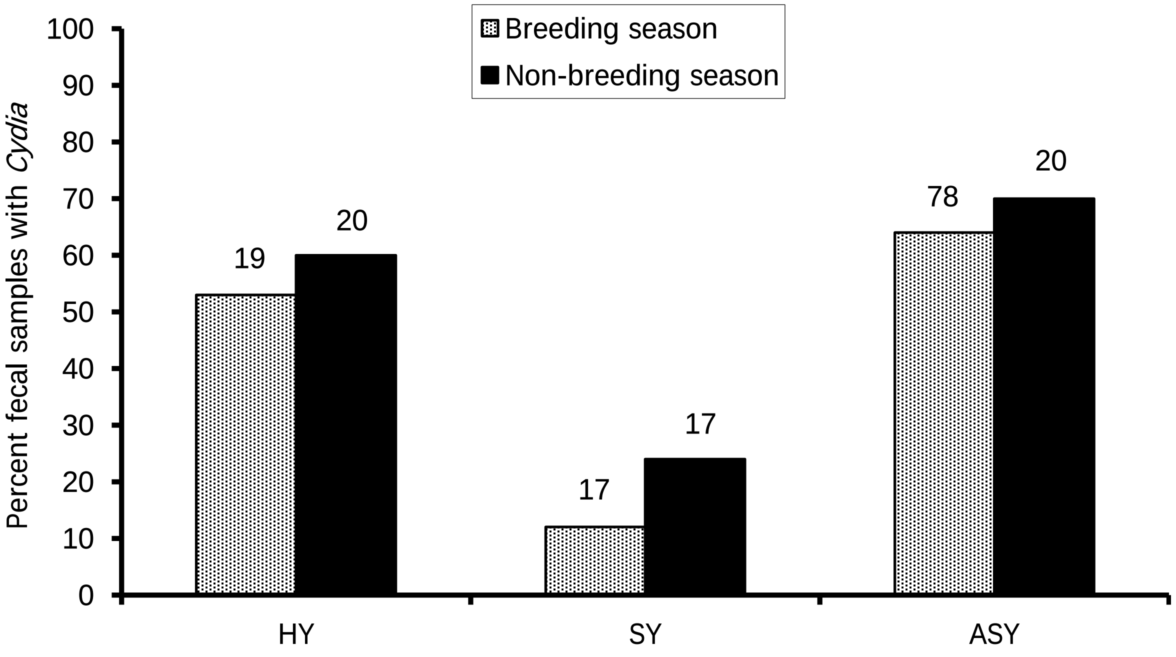

Figure 14.3. Percent of palila fecal samples containing *Cydia* fragments by season. Sample sizes are shown above bars. HY = hatch-year, SY = second-year, ASY = after-second-year. There were no significant differences within any age class (Fisher's exact test, $P > 0.05$).

and $P = 0.005$, respectively) but not significantly more often than in HY samples ($P = 0.532$; Figure 14.4).

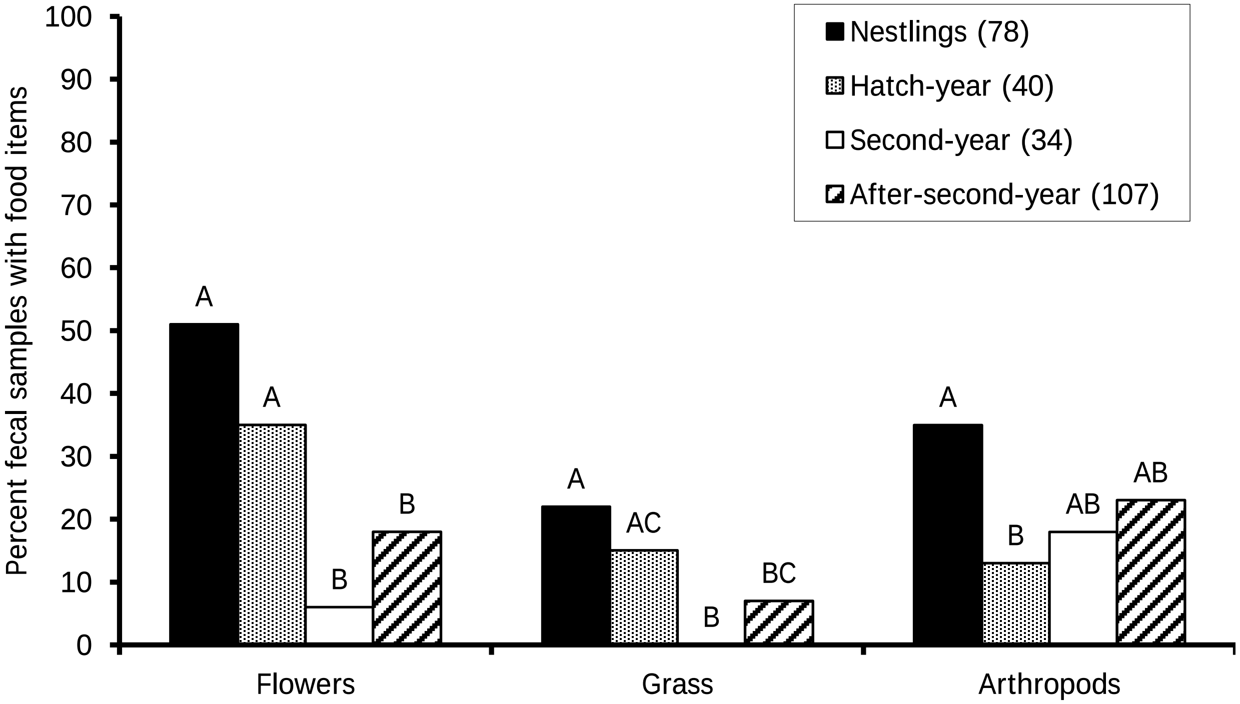

Figure 14.4. Percent of palila fecal samples containing flowers, grass, or arthropod fragments by age class. Sample sizes are shown in parentheses. Different letters above bars indicate a significant difference within each food category (Fisher's exact test, $P < 0.05$).

Fragments of arthropods other than *Cydia* were detected in the feces of all age groups. These fragments included legs of spiders (Araneae) and hemipterans (plant hoppers and true bugs), as well as fragments of heads and mandibles of larger caterpillars, such as *Scotorythra* spp. (Lepidoptera: Geometridae). Fecal samples of N birds contained relatively more arthropod fragments than did those of SY or ASY birds, although this difference was not significant ($P = 0.107$ and $P = 0.130$, respectively). Fecal samples from HY birds contained fewer arthropod fragments; the incidence was significantly lower than it was for N birds ($P = 0.016$) but was not significantly different from that of SY or ASY birds ($P = 0.767$ and $P = 0.216$, respectively; Figure 14.4).

Discussion

The palila diet consists largely of māmane seeds. Like many granivorous and frugivorous birds, palila rely on high-protein foods, such as insects and spiders, to supplement their diet (e.g., Skutch 1945, Kalmbach 1958). Arthropods are particularly important to developing chicks and adult females during the breeding season (Martin 1987, Verhulst 1994) when protein requirements are highest. Our results indicate that insects compose a greater proportion of the nestling diet than the diets of other age groups. Nevertheless, no difference was found in the composition of adult diets between the breeding and non-breeding seasons.

Cydia caterpillars feed within the seeds of māmane pods where they spend their larval life (Oboyski 2011). To be consumed by foraging birds, caterpillars must be extracted from māmane pods, but they may be found incidentally by birds ripping open pods to access seeds. Hatch-year palila require several months of foraging with adults before they are competent at obtaining māmane seeds (Miller 1998, Banko *et al.* 2002). Presumably, second-year birds perfect their foraging techniques by the time they become adults.

Nestling palila consumed *Cydia* caterpillars at the highest rate. *Cydia* fragments were found in the feces of virtually all palila nestlings but in less than two-thirds of adult birds. Nestlings are dependent on adults for all of their food, indicating that adult palila are feeding caterpillars to their chicks more frequently than consuming this food themselves. Of all age classes, second-year palila consumed *Cydia* least frequently, suggesting that they have not yet learned to search or forage effectively for caterpillars within māmane pods. Nevertheless, second-year palila consume other arthropods about as frequently as do other age groups, suggesting that insects found on foliage and branches are exploited equally by all ages.

Other foods, such as flower stamens, grass seeds, and arthropods other than *Cydia*, were found more often in feces of nestlings than in other age groups. The flower part most often recognized in palila feces was the stamen of māmane, which is a source of protein-rich pollen. Grass seeds were also found in palila feces. Though grass seeds may not be a particularly rich source of protein, they may provide other nutrients not found in māmane seeds. Arthropods, such as spiders, plant hoppers, and caterpillars other than *Cydia*, represent packets of protein and fats not found in plants and may be important as supplements to the palila's usual diet of māmane seeds. Perkins (1903) found the stomachs of several palila to be full of larvae of *Uresiphita polygonalis virescens* (Crambidae), but we found no indication of *Uresiphita* in the diets of birds we sampled.

Auxiliary food items were most often recovered from nestling samples, suggesting that other age groups rely more on māmane seeds. However, various foods may pass through the digestive tracts of nestlings at rates different from older birds, possibly affecting comparisons of diet composition among age groups. Regardless, auxiliary foods are clearly most prominent in the diet of nestling palila and least common in second-year birds. Understanding the diet composition of different age groups may eventually help explain differential survival rates of palila.

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15 FOOD CHEMISTRY

Paul C. Banko, Kevin W. Brinck

Introduction

If birds select foods based on their nutritional value, levels of toxins, or availability, then research into these topics will help us understand how to improve habitats for palila (*Loxioides bailleui*). The finch-billed palila specializes on seeds of māmane (*Sophora chrysophylla*), but it also eats māmane flower parts and leaf buds, in addition to other plant foods (Banko *et al.* 2002a). Additionally, palila prey upon caterpillars, particularly *Cydia* species (Tortricidae) that they find inside māmane pods. Caterpillars are especially important in the diet of nestlings, suggesting that māmane seeds may not be entirely suitable or adequate for growing young, even though they are a major diet component (Banko *et al.* 2002a, see Chapter 14: Diet). Furthermore, palila forage selectively among māmane seeds, preferring seeds from particular trees over others (U.S. Geological Survey unpublished data). This observation has led us to question whether palila might be responding to varying levels of nutrients or potential toxins. If this is the case, identifying patterns of seed chemistry will allow us to better understand the habitat requirements of this endangered species and develop strategies for its restoration.

Because of the palila's heavy dependence on foods derived from māmane, we investigated the chemical composition and variation within this species. A number of alkaloids have been identified from māmane seeds, leaves, and stems (Murakoshi *et al.* 1984), but the chemical composition of the palila's diet has not been investigated until recently. Our research focused upon answering two questions, 1) what are the nutritional rewards and possible toxic risks of eating māmane seeds and *Cydia* spp., and 2) does variation in chemical composition of seeds account for the palila's preference for seeds of particular trees?

Our first goal was to characterize the chemical composition of māmane embryos, seed coats, and *Cydia* caterpillars (Banko *et al.* 2002b). In that study, we pooled seeds from many trees to create a composite chemical profile of the palila's primary food. Because *Cydia* caterpillars eat only māmane seeds, we also determined whether they sequester any potential toxins that might be present in the seeds. To begin to address the question of whether palila select seeds based on alkaloid levels, we investigated variation in seed chemistry within trees and between trees during 2003−2009. We also evaluated changes in seed chemistry over time, both as the seed crop matured (within year) and from year to year. Initial results (2003−2004) indicated great variability among alkaloid levels in seeds collected in the same area on the same date; therefore, we attempted to determine the feasibility of controlling for some sources of variation by evaluating seasonal and annual variability of seed alkaloid levels within trees. We also investigated alkaloid variability between seeds within individual pods.

Methods

To determine the gross composition of nutrients and potential toxins in māmane seeds, we collected seeds during 4–18 August 1999 along a gradient of elevation extending from 1,750–2,820 m on the western slope of Mauna Kea (Banko *et al.* 2002b). Palila occur throughout the area where we collected seeds. August represents a time when all age classes of birds, including nestlings and fledglings, are usually consuming seeds. We arbitrarily picked 6–34 full-sized, green pods from 75 trees (≥2 m tall and ≥2 m wide) at 15 stations (five trees/station) each separated by 76 m of elevation. Pods were assigned relative ages based on their coloration, and we recorded seed coat and embryo color to complement this information

(Table 15.1). Pods (n = 1236) contained 1–10 expanded seeds each, but some seeds were partially or entirely eaten by *Cydia* caterpillars. We extracted seeds that were expanded (≥3 mm across the widest portion of the short axis) from the pods, removed the seed coats, packed the embryos and seed coats separately in vials, and flash-froze (liquid nitrogen) the samples within an hour of picking the pods. Samples were transferred to an ultracold (-70°C) freezer, then again to a nitrogen dry-shipper before being sent to Dr. Martin Cipollini at Berry College, Berry, GA, for gas-liquid chromatography-mass spectrometry (GLC-MS) and nutrient analyses, including protein, lipid, and mineral content.

Table 15.1. Size and color classes used to categorize the developmental stage of pods and seeds collected for chemical analysis.

Developmental stage[1]	Seed coat & embryo color[2]
YP = Young pod (seed <3mm; pod bright green)	W = White (usually in YP pods)
RP = Ripe pod (seed ≥3mm; pod bright green)	G = Green (typical of YP, RP, AP pods)
AP = Aging pod (seed ≥3mm; pod grayish-green)	Y = Yellow (typical of RP, AP, MP pods)
MP = Mature pod (seed ≥3mm; pod <50% brown)	O = Orange (typical of MP pods)
SP = Senescent pod (seed ≥3mm; pod = 50% brown)	D = Dark (decaying; found in any pod stage)

[1] Seed coat pliable (not hardened) in all stages

[2] Color codes in combination designate intermediate hues, with predominant color listed first.

We collected 200 *Cydia* caterpillars from māmane pods between 2,000 and 2,500 m elevation on the western slope of Mauna Kea during September–November 1995. Specimens were flash-frozen in liquid nitrogen within five minutes of being extracted from pods. A second group of 209 caterpillars, collected during May–July 2000, was fasted for 24 hours to clear their guts of māmane seed tissue before being flash-frozen. See Banko *et al.* (2002b) for details of chemical analysis of māmane seeds, seed coats, and caterpillars.

To determine the variability in the specific chemistry of embryos within pods and trees, between different trees, and over time, we collected embryos (seed coats removed) from marked phenology trees (Banko *et al.* 2002c; see Chapter 16: Food Availability: Māmane Phenology and *Cydia* Caterpillars) on two western slope palila study grids (PL Mauka and PL Makai; Figure I.1), during April−May and July 2003 and May and August−September 2004. Pods were not generally available on phenology trees in Manao and Ahumoa study grids in 2003, and we did not collect pods from these trees in 2004. We collected 197 embryos in 2003 and 151 embryos in 2004 from a wide range of pods and trees (Table 15.2).

Table 15.2. Numbers of samples collected for analysis of the variability of specific chemical compounds.

Sample	April−May 2003	July 2003	May 2004	August−September 2004
Trees	24	18	50	38
Pods	55	18	125	50
Embryos	150	47	151	59

To begin evaluating variation in chemistry within individual trees, we analyzed a subsample of seeds from the trees that were sampled in April (*n* = 12) and May (*n* = 42) of 2003. We arbitrarily collected pods with at least one expanded seed (≥3 mm as measured across the broad surface of the pod), but we usually selected pods with two or more seeds to facilitate analyses of intra-pod variation in chemistry (see below). As in 1999, we assigned relative age categories to pods based on size and color (Table 15.1). Whenever possible, we selected pods that were bright green, suggesting that they were at an early developmental stage and likely to be very attractive to palila (see Chapter 13: Habitat Use and Foraging Patterns). We recorded the quadrant of the tree (N, E, S, W) from which pods were collected. For each pod, we recorded the number of expanded seeds and signs of *Cydia* caterpillars (e.g., emergence hole, pupal case, frass inside the pod). When a caterpillar was found inside a pod, we measured its length (to the nearest one millimeter) and estimated the amount of embryo it had eaten.

Caterpillars were not collected (except in 1995 and 2000), although we did collect the remains of embryos that were partially eaten. For each seed within a pod, we recorded seed coat and embryo color (Table 15.1) and measured diameter to the nearest 1 mm before removing the seed coat and placing the embryo in a microcentrifuge tube. Each microtube of embryos was labeled, sealed, and flash-frozen in liquid nitrogen (nitrogen dry-shipper) as soon as the last embryo was extracted from the pod (usually within 10 minutes of picking the pod). Beginning in July 2003, we stored each embryo in a separate microtube and designated its relative order within the pod. The 2004 methodology was otherwise the same as earlier years.

To initially assess variation within and among individual pods of the same tree, we analyzed all embryos (seed coats removed) from a subsample of pods collected in April–May 2003 (*n* = 42 pods), July 2003 (*n* = 18), and May 2004 (*n* = 15).

We expanded our investigation of within-pod and within-tree variation in alkaloid levels during 2007–2009, when we collected seeds from nine māmane trees in mesic native forest recovering from long-term ungulate damage in Kīpuka Puaulu (1,220 m elevation) on Mauna Loa Volcano, Hawai‘i Volcanoes National Park, Hawai‘i Island. Trees were similar in size (3–5 m height) and relative vigor, they were spaced within 30 m of one another and they yielded relatively light crops of pods that were at a similar stage of development.

We evaluated temporal changes in seed alkaloid levels by sampling from the nine trees at monthly intervals: 7 June, 5 July, 3 August, and 31 August 2007. To assure that seeds were sampled along a consistent chronosequence, in each tree we marked one cluster of pods that were at a similar stage of development both within the cluster and among clusters on other trees. Developmental stage was assessed by pod color and the degree of seed expansion. Sampled pods contained at least one expanded seed, were entirely or mostly green, and were judged to be potentially attractive as food to palila, although palila are not known to have inhabited this region. Two exceptional cases were pods that had turned brown and whose seeds had hardened, conditions that palila tend to avoid when foraging. Each month, we arbitrarily picked one pod from each tree's cluster, and we collected the first expanded seed (≥3 mm across the broad side), which we defined as the seed proximal to the pod stem. We recorded the number of expanded seeds in each pod as well as pod color before measuring the diameter and noting the color of the first seed. We cut the seed coat and gently extracted the embryo into a small plastic vial, which was placed in a container of frozen CO_2 within 10 minutes of having picked the pod. In a few instances, we collected the second or third seed because *Cydia* caterpillars had eaten all or part of the embryo or because the embryo was underdeveloped. All seeds were collected during afternoon hours and were placed in an ultra-cold freezer (-56°C) within 1.5 hours of collection.

To evaluate annual and within-pod variability in seed chemistry, in July 2009 we collected all the seeds of a single pod picked from any branch on three of the nine marked trees having any suitable pods. Seed processing and storage procedures were similar to those used in 2007.

Results

Māmane Seeds

We confirmed the identity of about 15 potentially toxic alkaloids and phenolics, in the extract of māmane embryos from our 1999 sample (Banko *et al.* 2002b). Major constituents included cytisine, 5,6 dehydrolupenine, lupenine, and anagyrine, which together comprised about 88% of the total alkaloids. These data confirm the presence of significant levels of quinolizidine alkaloids in māmane embryo tissues fed upon by palila and *Cydia* caterpillars. We did not identify the specific phenolics.

The analysis of seeds collected in 1999 indicated that compared to seed coats, embryos contained slightly less non-structural carbohydrate and trace minerals but much higher levels of total lipids, total protein, and most major minerals (Figure 15.1). Reflecting their higher level of total protein, māmane embryos were much higher than seed coats in all amino acids measured. Amino acid profiles for embryos were relatively balanced, ranging from glutamate at 5.5% to methionine at 0.28% dry mass. We detected no non-protein (toxic) amino acids in our analysis. Embryos were much lower than seed coats in non-digestible fiber (9.47% vs. 57.55% respectively, based upon subtraction of all measured nutrient and secondary chemical constituents from 100%).

Compared to seed coats, māmane embryos contained much higher levels of all major alkaloids as well as several other individual metabolites; embryos also contained about four times greater levels of total alkaloids (about 4% of dry mass; Figure 15.2). Our analysis found the opposite for total phenolics; embryos were nearly eight times lower in total phenolics than seed coats, where they were about 4% of dry mass.

Comparison of Māmane Embryos and *Cydia* Larvae

In comparison with māmane embryos, whole unfasted *Cydia* larvae contained slightly lower amounts of total sugars, but higher amounts of total lipid and total protein (Banko *et al.* 2002b; Figure 15.1). Non-digestible fiber in *Cydia* was essentially zero, in that our estimates of major nutrients exceeded 100% when summed. Due to insufficient sample material, we did not assay *Cydia* for minerals.

The sample of unfasted *Cydia* larvae from September–November 1995 contained approximately five times as much total phenolics as did māmane embryos from August 1999 (Figure 15.2). These levels (about 3%) were similar to the levels found in māmane seed coats. However, larvae contained much lower levels of alkaloids than did embryos. Total alkaloid content of *Cydia* larvae was 0.087% of dry mass, which was about 50 times lower than that of māmane embryos. Sparteine, N-methylcytisine, cytisine, 5,6-dehydrolupenine, rhombifoline, lupenine, matrine, and anagyrine were found at levels of 0.001–0.002% of dry mass, along with numerous apparent break-down products at similarly low levels (data not presented). Residual alkaloids and break-down products were largely eliminated with fecal matter, as total alkaloid

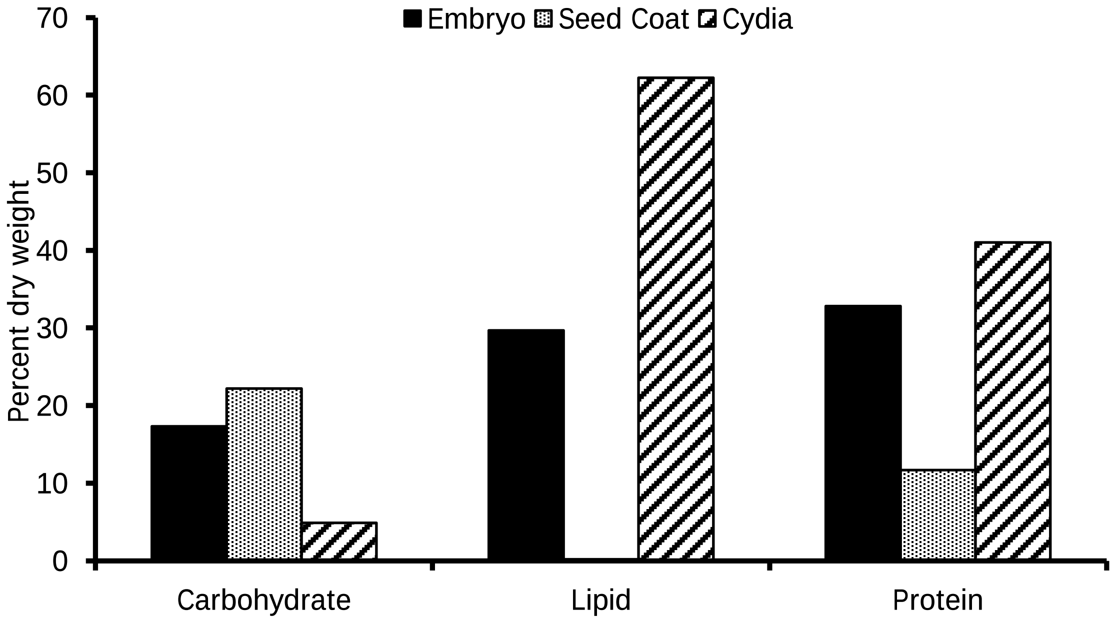

Figure 15.1. Distribution of nutritional components among māmane embryos, māmane seed coats, and *Cydia* caterpillars during August 1999 on the western slope of Mauna Kea, Hawai'i. Constituent values total >100% for *Cydia* because we used only the Bradford method of quantifying protein, which produced higher values compared to other methods used for embryos and seed coats (see Banko *et al.* 2002b for details).

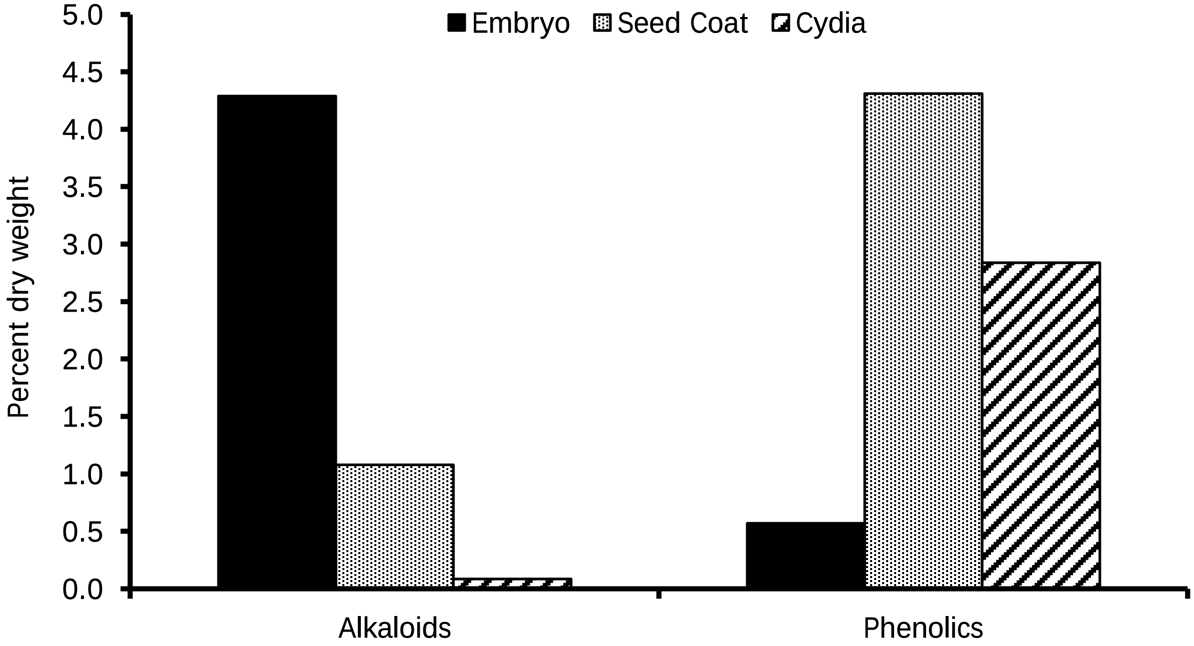

Figure 15.2. Distribution of secondary compounds among māmane embryos and seed coats and unfasted *Cydia* caterpillars during August 1999 on the western slope of Mauna Kea, Hawai'i.

levels were reduced to a level (0.019%) about eight times lower during the 24-hour fasting period.

The only identifiable alkaloid in the sample of starved *Cydia* was sparteine at 0.002% of dry mass. Altogether, alkaloid levels in fasted larvae were about 200 times lower than levels in seed embryos, suggesting that these insects do not sequester alkaloids in their tissues while feeding upon māmane.

In 2004 and early 2005, the embryos collected in 2003–2004 were subjected to gas chromatographic analysis at Berry College, Georgia. This analysis identified 17 distinct chemicals present in almost all embryos (Table 15.3). Only seven of those chemicals were present in sufficient concentrations to be meaningfully analyzed (M. Cipollini, personal communication).

Table 15.3. Quinozidoline alkaloids (and other chemicals) isolated from māmane embryos from Mauna Kea, Hawaiʽi, with gas chromatograph retention times (minutes), which indicate the time taken by each compound to come out of the microcapillary column during the analytical process. Compounds marked with (*) were present in concentrations sufficient for significant measurement.

Chemical	Retention time
sparteine	13.80
11,12-dehydrosparteine	14.64
ammodendrine	14.91
lusitanine	15.05
n-methylcytisine*	15.97
cytosine*	16.38
unknown 1	16.92
unknown 2	16.92
unknown 3	17.18
5-6 dehydrolupenine*	17.85
rhombifoline*	18.00
lupenine*	18.20
11-allylcytisine	19.00
matrine*	19.28
anagyrine*	20.36
unknown 4	20.68
baptifoline	22.46

Embryos from 10 of the 42 pods sampled in April 2003 were analyzed separately to compute within-pod variation (Table 15.4). The weighted variances of alkaloid levels were calculated from all seeds or seed fragments (less four seeds <2 mg weight), and these results were used to estimate within-tree and between-tree variation. It is possible that fragments from different seeds became mixed, but the result would have been to bias within-pod variation downward. Comparing the total alkaloid within-pod variation to the across-tree variation identified a significant difference ($F_{2,21} = 11.14$, $P < 0.001$). The between-tree variation was not

Table 15.4. Variation in alkaloid content in māmane embryos at three different ecological scales on the western slope of Mauna Kea, Hawai'i. Variance units are µg of alkaloid per gram of dry seed mass squared.

	Between tree	Within tree	Within pod
sparteine	—	—	—
unknown 1	15.2	1.4	1.7
n-methylcytisine	5.4	12.0	4.5
cytisine	81.9	52.0	15.9
unknown 2	52.9	6.8	9.7
5-6 dehydrolupenine	22.9	9.6	20.7
rhombifoline	8.3	6.2	6.3
lupenine	294.6	21.3	5.8
matrine	11.1	4.4	4.3
anagyrine	79.0	75.3	18.2
Total alkaloids (including unknowns 1 & 2)	5,384.5	3,358.6	301.4

significantly larger than within-tree variation ($F_{24,2}$ = 1.60, P = 0.227), but the power to detect a difference was low, as we collected multiple pods from only three trees.

In 2003 we detected two unknown chemicals that were closely related (regression t_{72} = 15.12, P < 0.001); their levels were more closely correlated than any other two components. They possibly represented two peaks of the same chemical, non-alkaloids, or perhaps a by-product of the extraction process. This latter supposition was supported by a factor analysis that identified the major components of variation. The main factor, accounting for 34% of the variation, was a combination of the identified alkaloids while the second factor, accounting for an additional 24% of the variation, was almost entirely composed of unknowns 1 and 2. In other words, the two unknowns seem to be completely unrelated to the identified alkaloids. Subsequent analysis in 2004 and 2005 identified two more unknowns. The original unknowns, 1 and 2, may actually have been a double signal of the same chemical (M. Cipollini, personal communication). The unknown chemicals might be identified by mass spectrometry, but we did not undertake this analysis.

From the analysis of samples (n = 7 trees) obtained from Mauna Loa in 2007, we found that mean total alkaloid levels peaked in July but with considerable variability (Figure 15.3). Mean cytisine levels increased from June to July and then decreased after August (Figure 15.4). Alkaloid levels in the two hardened seeds that were collected from brown pods were similar to levels in seeds of green pods that also were sampled in early August.

Overall alkaloid levels in our small point sample in July 2009 revealed little annual variation among the trees that also were sampled in 2007. General alkaloid levels of seeds within pods (n = 3) varied by up to an order of magnitude. Levels of cytisine and some other alkaloids were even more variable. There was no apparent relationship between alkaloid levels and the position of seeds within the pod. Neither was there any evidence that alkaloid levels were related to the number of expanded seeds per pod.

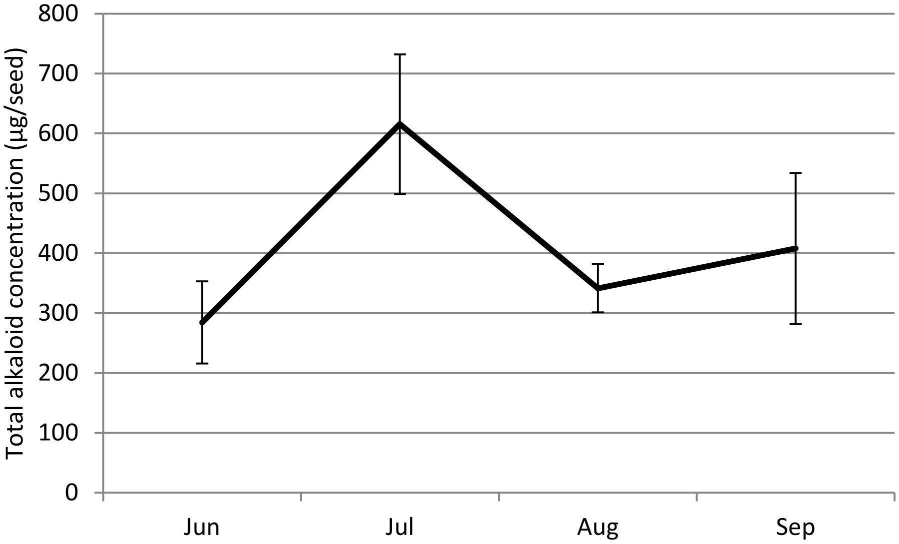

Figure 15.3. Seasonal trend in the concentration (µg per seed) of total alkaloids in māmane seeds on Mauna Loa, Hawai'i, 2007.

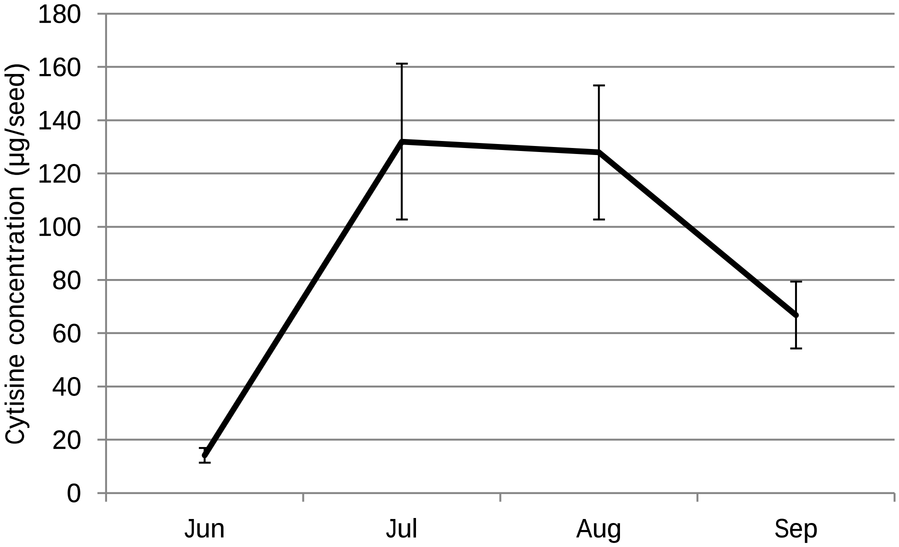

Figure 15.4. Seasonal trend in the concentration (µg per seed) of cytisine in māmane seeds from Mauna Loa, Hawai'i, 2007.

Discussion

Why do palila commonly feed on māmane embryos while consistently excluding seed coats? Based upon our work, embryos at the stage consumed by palila contained high levels of several alkaloids, including the highly toxic quinolizidine cytisine, which exceeded 1.5% of seed dry mass (Banko *et al*. 2002b). Embryos contained about 4% total alkaloids, whereas seed coats had lower levels of the same major alkaloids (about 1% total alkaloids). Because embryos contained levels of alkaloids known to cause severe neurological symptoms and death in humans and other animals (Keller 1975), it is likely that palila have evolved some degree of tolerance to the alkaloids in this species. Based upon an estimated daily consumption rate of 300 seeds per adult palila (U.S. Geological Survey unpublished data), we calculated a total daily alkaloid intake of about 12,000 mg/kg body mass. This value far exceeds oral LD_{50} estimates for small granivorous animals such as mice (Banko *et al*. 2002b). The tolerance of palila to such high levels of alkaloid may be the product of intestinal uptake followed by detoxification in the liver (with consequent effects on relative liver size), non-absorption from the gut (unlikely because quinolizidines are lipophilic under alkaline conditions of the gut and should diffuse into the body), or active export via P-glycoprotein-type ABC transporters (Banko *et al*. 2002b).

Relative to embryos, seed coats had higher levels of phenolics and fiber, but lower levels of most major nutrients. It is thus likely that seed coats are rejected because of lower overall nutritional value, coupled perhaps with a negative influence of phenolic-based secondary metabolites. Phenolic compounds, such as tannins and phenolic glycosides that may be found in the seed coats of legumes, can be toxic or astringent or may affect digestion by binding to protein and other complex molecules (Levey and Cipollini 1999).

Alkaloid levels in the two hardened seeds that were collected from brown pods were similar to levels in seeds of green pods that were sampled at the same time in early August. This suggests that palila may reject brown pods more on the basis of their toughness than because of seed toxicity. Additionally, palila may occasionally open brown pods to extract *Cydia* caterpillars that are sometimes found within. Oboyski (2011) found live mature larvae in hollowed-out, dry mature seeds, while in the laboratory some larvae survived for more than 18 months in drying seeds and emerged as adults shortly after the application of a moist tissue, suggesting the capacity for facultative diapause.

Māmane embryos seem extremely well-balanced nutritionally and contain relatively low levels of fiber and high levels of carbohydrate, lipid, and protein (a ratio of about 1:2:2), as well as relatively balanced profiles of essential amino acids and minerals (Banko *et al.* 2002b). For example, based on our estimate of daily seed consumption, the amount of nitrogen and protein consumed is respectively about 14 and 9 times that required for maintenance in granivorous birds (Banko *et al*. 2002b). While variation in digestive efficiency is not considered in these estimates, and we do not have an estimate of nitrogen and protein requirements for palila, it is unlikely that palila have difficulty obtaining sufficient protein or other nutrients from māmane seeds. Although we did not assay minor organic constituents, such as vitamins, we can say that, exclusive of possible toxicity due to alkaloids, māmane embryos are particularly well-balanced nutritionally, thus largely explaining why palila rely so heavily on māmane embryos for their daily diet and for rearing their offspring. We hypothesize that palila evolved specialization on māmane as a result of food competition with other seed-eating honeycreepers (Drepanidinae) in relatively simple habitats that were dominated by only a few tree species.

Why do palila commonly supplement their diets with *Cydia* larvae? In addition to being found conveniently inside māmane pods, our data suggest that these insects are relatively non-toxic sources of lipid, protein, and other nutrients, and thus represent occasional but relatively high-quality resources for the bird. Adults likely seek out *Cydia* to feed to their chicks, as the incidence of *Cydia* mandibles is very high in nestling and fledgling fecal samples (see Chapter 14: Diet). Relatively non-toxic, nutritious foods would be important to the survival and development of birds that were susceptible to alkaloid toxicity. The frequency of *Cydia* mandibles is also higher in fecal samples collected from adults than in samples from juvenile birds that are independent of parental care, suggesting that experience may be helpful in finding pods containing larvae. For example, birds may learn to identify pods that contain *Cydia* by the presence of silk caps that are spun by the larvae over their emergence holes, and they may learn that some trees support larger infestations of larvae than do others. Although *Cydia* larvae have a much higher level of phenolics than do seed embryos, total phenolics in the insects were close to the level found in seed coats. Thus, the idea that phenolics might induce palila to reject seed coats must be tempered by an understanding of the relative nutritional rewards. Assuming that the phenolics within *Cydia* bodies are of māmane origin and have similar anti-nutritional effects when consumed by palila regardless of the food source, seed coats should be nonetheless far less nutritious than are *Cydia* larvae.

Our data suggest that *Cydia* larvae break down the alkaloids in the course of digestion, as evidence of alkaloids and break-down products is found primarily in insects containing material within the gut. We found no evidence that *Cydia* larvae sequester significant quantities of these alkaloids in their bodies, and the lack of toxin sequestration is compatible with their cryptic appearance. Furthermore, crypsis may reduce predation by palila since pods often contain larvae that have consumed one or more embryos, and are thus relatively exposed to foraging birds.

Are non-specialist birds and other generalist seed predators more susceptible to māmane seed alkaloids than are palila and *Cydia*? In other words, is there any evidence for evolved tolerance in these specialist species? Because the palila is an endangered species, it is not possible to compare the palila and other Hawaiian honeycreepers in terms of their tolerance to quinolizidine alkaloids. Nevertheless, controlled feeding trials with other species might indirectly address part of the question. We have been unable to find published reports on oral toxic effects of quinolizidines on wild birds; however, four 10–14-day-old, hand-reared house finches (*Carpodacus mexicanus*), convulsed and died within about 10 minutes of ingesting mashed māmane seeds (C. Kuehler, San Diego Institute for Conservation Research, personal communication). Assuming that a suitable laboratory diet could be developed, feeding trials comparing the tolerance of *Cydia* and related moth species to alkaloid levels would seem more feasible.

Do *Cydia* compete with palila for māmane seeds, and what are the consequences of this interaction? Answers to these questions may help explain the evolutionary impact on māmane of seed predation by palila and *Cydia*. There may also be practical benefits if understanding the variation in seed chemistry improves our ability to manage habitat for palila and other native species. It is possible that individual māmane trees vary significantly in their seed alkaloid profiles, due to both genetic and environmental effects. For example, samples of seeds collected from two different individual māmane plants in Hawai'i have been reported to contain virtually no cytisine, instead being dominated by anagyrine, N-methylcytisine, and baptifoline (Pena and Cassels 1996), whereas our bulk sample derived from many individuals was dominated by cytisine (Banko *et al.* 2002b).

Both palila and *Cydia* feed heavily within certain trees and lightly upon others, and additional research might identify factors that influence the selection of individual māmane by consumers. Are seeds of heavily-exploited individuals particularly high in certain required nutrients (lipids, carbohydrates, protein, essential amino acids, etc.) or are they particularly low in certain toxic secondary metabolites? Additionally, what environmental factors contribute to variability in seed chemistry? We were unable to relate the pattern of increasing then decreasing levels of cytisine during summer to environmental conditions, although we did not examine rainfall patterns. Similarly, we did not consider whether rainfall or other factors might account for the relatively minor annual variation in the seed chemistry of individual trees. Our analyses of variation in seed alkaloid levels, though limited, suggest that many trees must be sampled to address the question of whether toxic secondary metabolites can account for preferences by palila or *Cydia*.

Despite challenges in determining the bases for variability in māmane seed chemistry, the synthetic pathways of the quinozidoline alkaloids suggest testable hypotheses about the relative alkaloid concentrations in māmane seeds. Both lupenine and anagyrine are intermediates in the chemical synthesis of multiple alkaloids (Table 15.5). Lupenine, for instance, can be converted to either matrine or one of several other chemicals, suggesting the possibility that trees producing seeds with matrine might produce less of other alkaloids. Similarly anagyrine can be further processed into rhombifoline or cytisine. Concentrations of intermediate chemicals might remain relatively constant while a seed is growing and alkaloids are being synthesized. As a seed matures, concentrations of the intermediate would decrease and those of end products would increase.

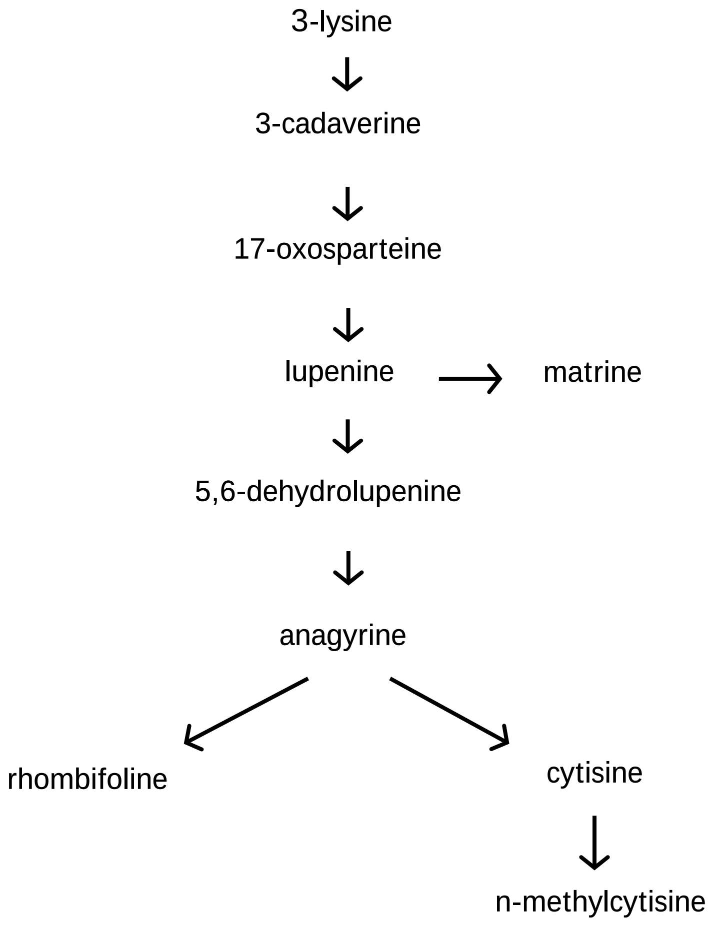

Figure 15.5. Presumed biosynthetic pathway for the major alkaloids in *Sophora chrysophylla*. Figure from Neal *et al*. 2005.

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16 FOOD AVAILABILITY: MĀMANE PHENOLOGY AND *CYDIA* CATERPILLARS

Peter T. Oboyski, Paul C. Banko, Luanne Johnson, Kevin W. Brinck

Introduction

Palila (*Loxioides bailleui*) feed primarily on the seeds of māmane (*Sophora chrysophylla*), and knowing when this food is available is important in understanding palila ecology and developing management strategies (Banko *et al.* 2009). Other major food items include māmane flowers and young leaves (flush) and *Cydia* spp. caterpillars that feed within māmane pods (see Chapter 14: Diet). To assess the availability of māmane pods, flowers, flush, and *Cydia* caterpillars along an elevation gradient we conducted phenology surveys in the dry, subalpine māmane forest on Mauna Kea above 2,200 m elevation.

Methods

We assessed the monthly production of flowers, pods, and foliage flush, and abundance of *Cydia* caterpillars on māmane trees from February 1998 through March 2001 on the southern and eastern slopes of Mauna Kea and through June 2005 on the northern and western slopes. No stations were sampled during March 1998. Samples stations were located along Hawai'i Forest Bird Survey transects at five elevations (2,200, 2,350, 2,500, 2,650, and 2,800 m). Four transects were selected from each side of the mountain, except in 1998 when three transects were selected randomly from each area. Within 100 m of each transect station, we selected five trees, each at least 2 m tall and 2 m across at the maximum crown width, using a random number table. Only three trees were sampled in 1998. A total of 335 trees (153 trees in 1998) were sampled each month (Table 16.1).

Table 16.1. Number of trees surveyed for phenology each month during 1998–2005 at five elevations on four sides of Mauna Kea. Numbers in parentheses are the sample of trees surveyed in 1998. No trees were available to survey at the lowest elevations on the east side. After March 2005, west side trees were surveyed quarterly.

Site	2,200 m	2,350 m	2,500 m	2,650 m	2,800 m	Total
West	20 (9)	20 (9)	20 (9)	20 (9)	20 (9)	100 (45)
North	20 (9)	20 (9)	20 (9)	20 (9)	20 (9)	100 (45)
East[1]	N/A	N/A	10 (6)	20 (9)	10 (6)	40 (21)
South[1]	15 (6)	20 (9)	20 (9)	20 (9)	20 (9)	95 (42)
Total	55 (24)	60 (27)	70 (33)	80 (36)	70 (33)	335 (153)

[1] Discontinued in March 2001

We estimated the productivity of each tree in terms of number of flowers, number of pods, and percent of live branch tips (meristems) with flowers, pods, and flush. We estimated tree height and canopy width to the nearest meter, percent of the tree that was alive, and percentage of yellowed (chlorotic) leaflets. Flowers and pods were counted individually on trees with little production and by groups of 3, 5, or 10 on trees in heavy production. All percent estimates (flowers, pods, flush, live biomass, chlorosis) used the categories 0, 0–1, 2–5, 6–10, 11–25, 26–50, 51–75, and 76–100%. At each elevation, we plotted the mean number per tree of flowers and pods as well as the percent flush to determine the overall seasonal availability and variability in these food resources.

To determine the incidence of *Cydia* larvae, we collected two pods from each tree. Pods were picked from a random location on the tree. If pods were not available on the tree being surveyed, they were picked from the closest tree with pods. A total of 10 pods (six pods in 1998) were collected from each station where pods were present, placed together in one bag with a label, and returned to the laboratory for dissection. We recorded the total number of seeds, number of seeds eaten by caterpillars, and number of *Cydia* caterpillars present for each pod. We calculated the average number of *Cydia* per pod along with the average number of pods per tree for each month to determine their relative abundance throughout the year.

This study was similar to the phenology study in the core palila habitat on the western slope of Mauna Kea (Banko *et al.* 2002a) with a few notable exceptions. This study circumscribed Mauna Kea from 2,200–2,800 m elevations, whereas the core habitat survey focused more closely on the western slope between 2,000–2,800 m, where nearly all palila were found. The trees in this study were selected at random each month, whereas trees in the Banko *et al.* (2002a) study were marked and revisited each month starting in 1989. For this reason, we do not compare the results of the two studies.

We also tracked the development of māmane pods from bud to senescence from December 1993 to April 1996. Individual stems were labeled and visited monthly to track their development. Average times were calculated to determine the development time between 1) the smallest detectable bud, 2) an open flower accessible for pollination and palila predation, and 3) a green pod suitable for seed extraction by a palila. We also calculated the length of time individual pods were available to palila as a food resource before turning dry and brown.

Results

The overall average number of māmane pods per tree from February 1998 to June 2005 was 64.6 ± 1.9 (mean ± SE), but pod abundance varied widely around the mountain (range = 0–8,050 pods/tree). Over the three-year period ending in March 2001, when data collection on the southern and eastern slopes was discontinued, mean pod production varied by up to 60% between slopes: 85.3 ± 6.7 pods/tree (south), 69.9 ± 9.0 pods/tree (east), 68.1 ± 5.0 pods/tree (west), and 50.9 ± 4.3 pods/tree (north). When all data collected through June 2005 were considered, the mean number of pods per tree on the western slope was 70.6 ± 3.0, reflecting higher overall productivity in these later years. In contrast, pod productivity on the northern slope over the entire study period was 50.9 ± 2.4.

We recorded seasonal peaks in māmane productivity. On the western slope, māmane flowers were most abundant from October to May in all years, followed shortly by the onset of pods from February through September (Table 16.1). Similar patterns of flower and pod production occurred on the three other slopes. New foliage flushed throughout the year on all four sides of the mountain. Peak annual flush occurred from June through October, although discrete peaks were discernable at other times (Figure 16.2). Pod production tended to be greatest at the higher elevations (Figure 16.3). The eastern slope could not be surveyed below 2,500 m after 1999; therefore, it was not comparable with the other slopes.

Pod production peaked in May−June at all elevations around Mauna Kea (Figure 16.4), but trees at higher elevations (2,650−2,800 m) yielded crops that were consistently larger (110−156%) than the overall seasonal mean (Figure 16.5). Trees at middle (2,350−2,500 m)

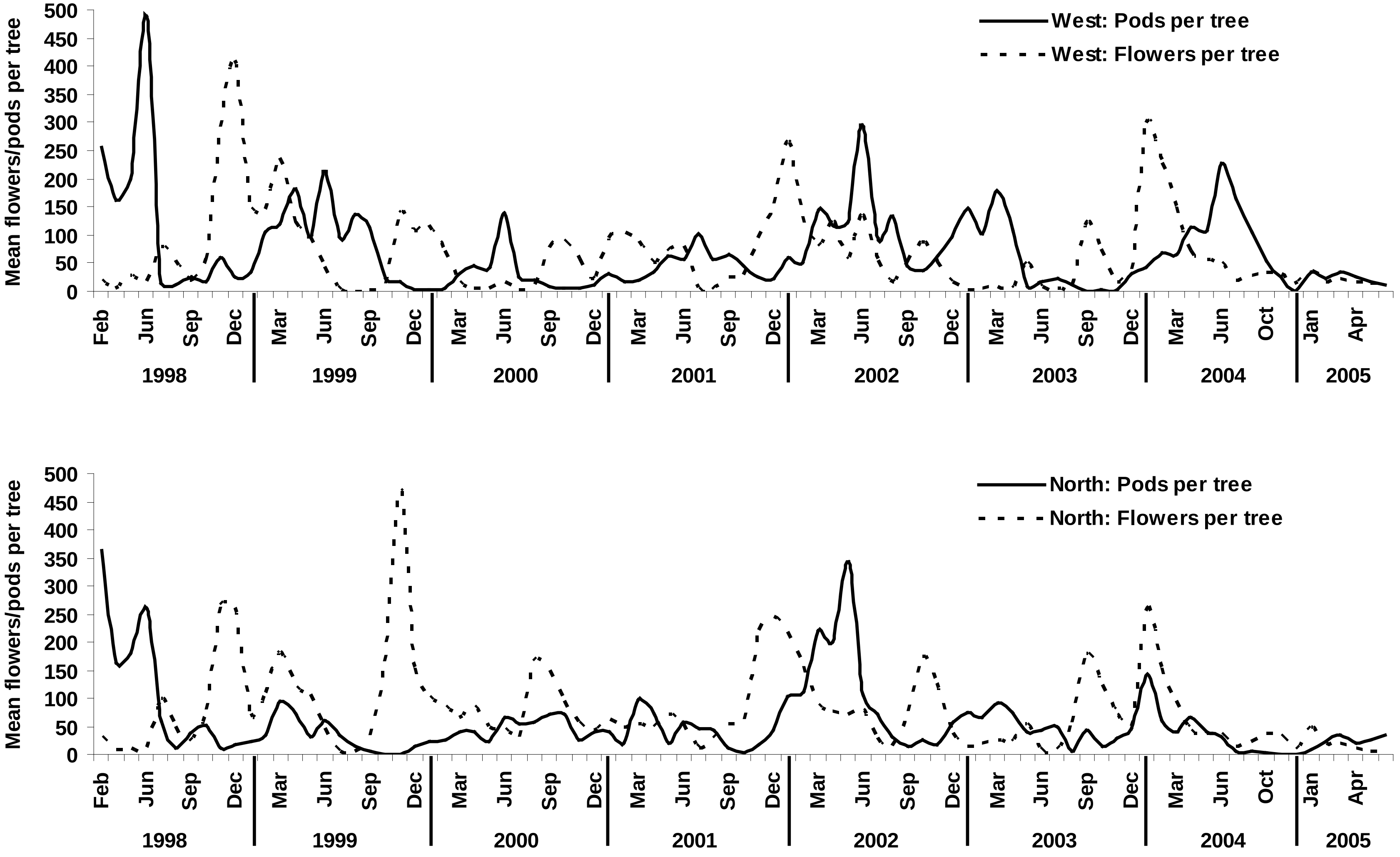
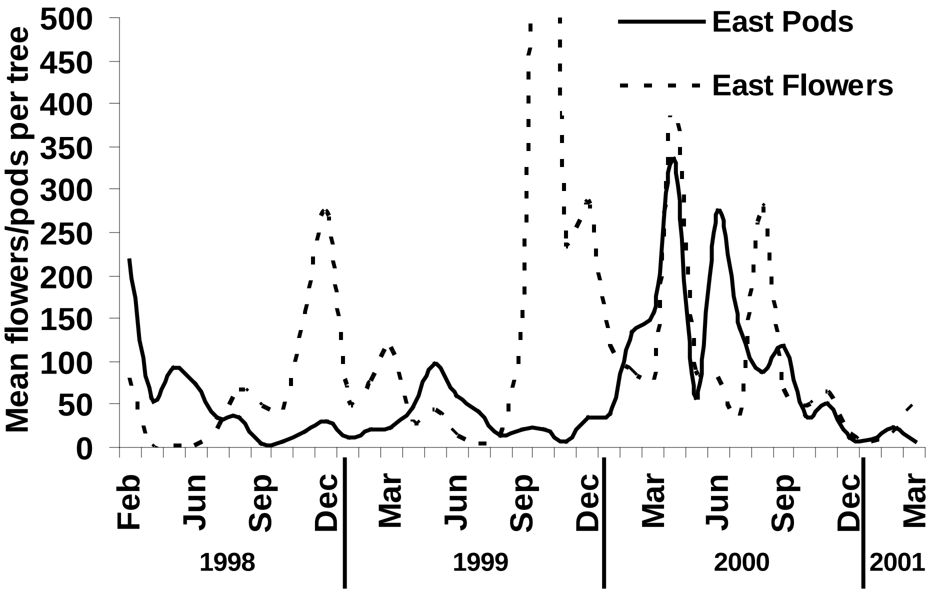


Figure 16.1. Māmane flower and pod production on the slopes of Mauna Kea, Hawai'i, from February 1998 to March 2001 (east and south) or June 2005 (west and north).



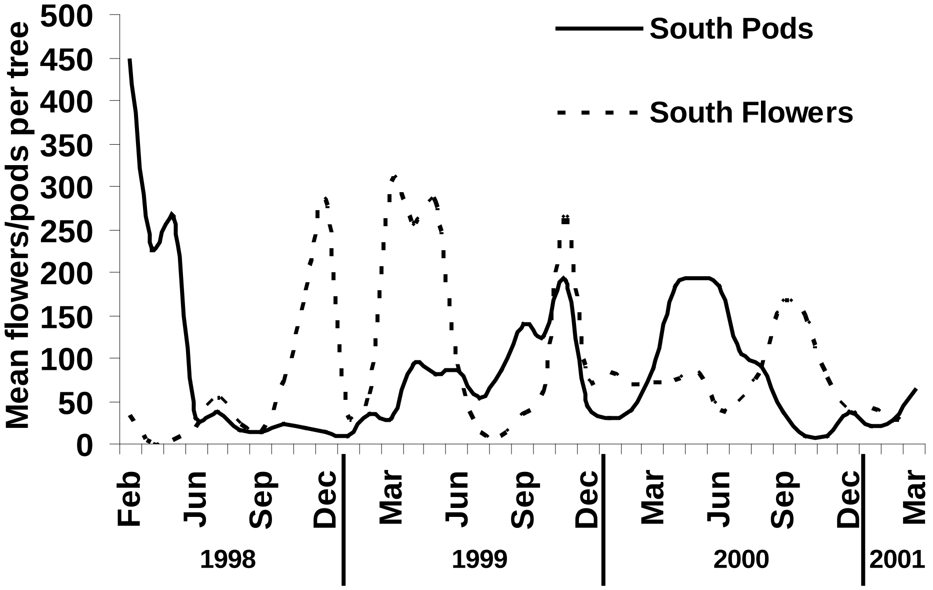


Figure 16.1 (continued). Māmane flower and pod production on the slopes of Mauna Kea, Hawai'i, from February 1998 to March 2001 (east and south) or June 2005 (west and north).

elevations produced slightly smaller (78–97%) crops than the overall mean, whereas low (2,200 m) elevation trees produced the smallest crops (18–85%). Therefore, high-elevation trees always yielded the most pods and low-elevation trees always yielded the fewest pods. The disparity in pod abundance along the elevation gradient was greatest during September–

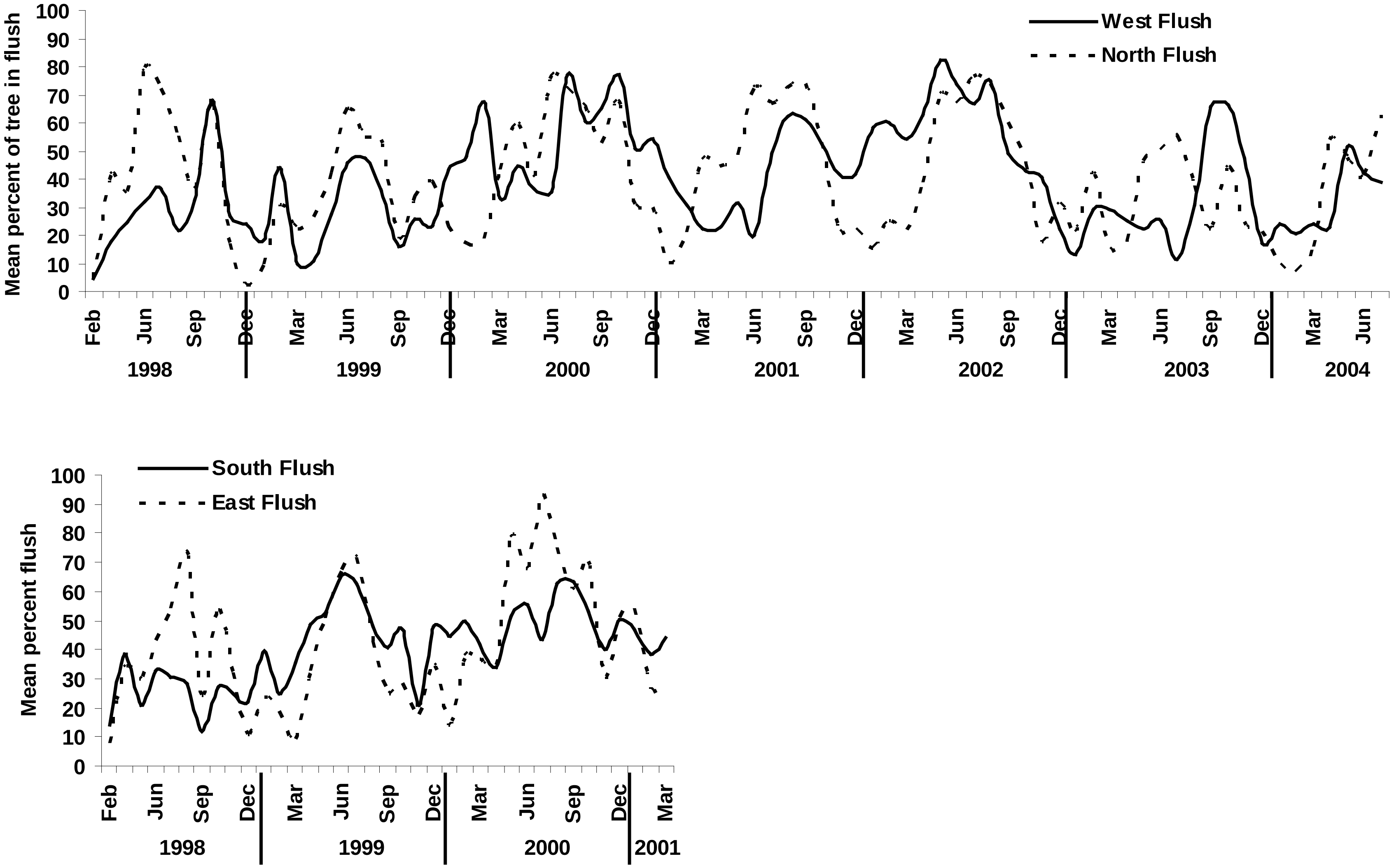


Figure 16.2. Māmane flush production (monthly average percent) on the four slopes of Mauna Kea from February 1998 to March 2001 (east and south) or July 2004 (west and north).

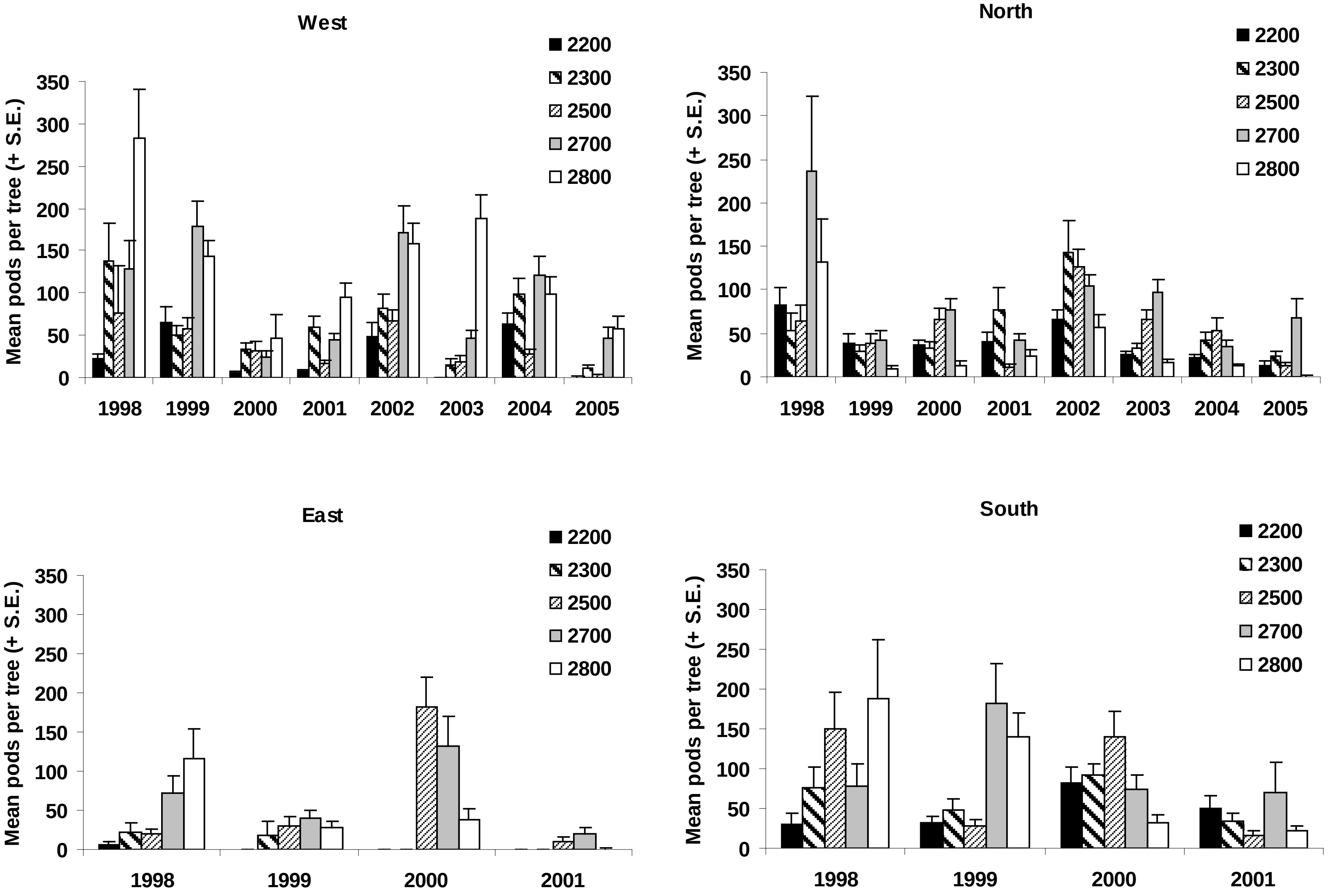


Figure 16.3. Māmane pod production by elevation in meters (yearly average with standard error [S.E.]) along the four slopes of Mauna Kea from February 1998 to March 2001 (east and south) or June 2005 (west and north).

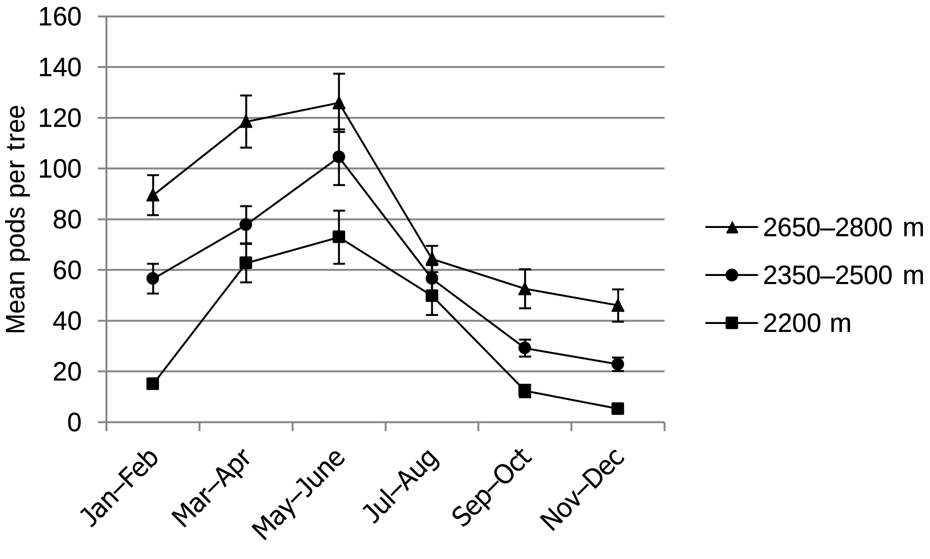


Figure 16.4. Seasonal variation in pod production (mean pods per tree ± SE) along a gradient of elevation on the four slopes of Mauna Kea from February 1998 to March 2001 (east and south) or June 2005 (west and north). Elevation strata are: low (2,200 m), mid (2,350–2,500 m), and high (2,650–2,800 m).

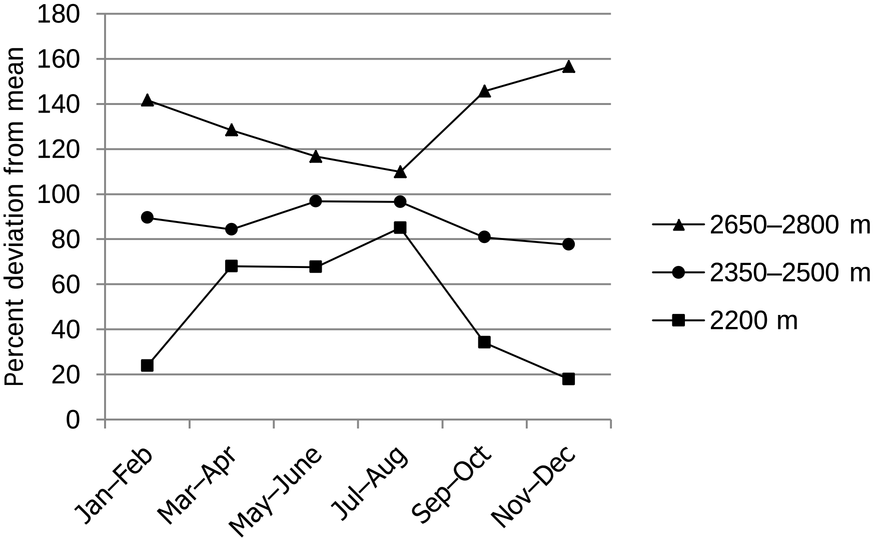


Figure 16.5. Seasonal deviation from the overall mean māmane pod crop size (pods/tree) along a gradient of elevation on the four slopes of Mauna Kea from February 1998 to March 2001 (east and south) or June 2005 (west and north). Elevation strata are: low (2,200 m), mid (2,350–2,500 m), and high (2,650–2,800 m). The data represent the percent deviation of pod yields from the overall mean crop in each stratum of elevation.

February, when high-elevation trees exceeded the overall mean crop size by 142–156% and low-elevation trees produced their smallest crops (18–34%).

Cydia abundance per pod varied over the course of the study (1998–2005). Caterpillar abundance around the mountain was greatest (0.162 caterpillars/pod) from September to January. The overall annual peak of *Cydia* abundance occurred in November with 0.195 caterpillars/pod. The average number of *Cydia* larvae per pod was usually greatest when the number of pods per tree was lowest (Figures 16.1, 16.6). Nevertheless, the annual peak in caterpillar abundance occurred in June, with an estimated average of 15.18 *Cydia*/tree (Figure 16.6), when considering peak annual pod abundance and peak caterpillars per pod. *Cydia* caterpillars were found year-round on all slopes, except for one month (November 1999) on the northern slope and two other months (June 1998 and February 2000) on the eastern slope. The mean development time from māmane bud to flower was 49.7 days (Table 16.2). Flowers required an average of about three months (98.1 days) to develop into an edible pod. We classified pods as edible by palila for another four months (132.2 days).

Discussion

The timing of flowering and seed set in māmane varies with elevation with flowers first appearing at higher elevations then moving down the mountain slope, as also reported by Banko *et al.* 2002a. Therefore, a large elevation gradient is necessary to assure an abundance of māmane pods, flowers, and *Cydia* caterpillars throughout the year for palila to exploit (Scott *et al.* 1984, Fancy *et al.* 1993, Lindsey *et al.* 1995, Banko *et al.* 2009). Palila densities are positively correlated with the number of māmane pods at different elevations (Hess *et al.* 2001), and the population is concentrated in areas containing large, mature trees (van Riper *et al.* 1978).

In this study, māmane pods were available around Mauna Kea throughout the year, although abundance varied seasonally and with elevation. Pods were always more abundant on trees at higher elevations, especially during September–February when pod crops at lower elevations were disproportionately small. Across all elevations, average pod availability per tree was greatest from February to September with peaks in April, May, and June. Therefore, māmane seeds are most available during the palila nesting season, which is generally March through September (van Riper 1980, Pletschet and Kelly 1990, Banko *et al.* 2002b). Māmane flowers and flush were more available during October–February, when māmane pods were less available to palila. Qualitative (presence-absence) data from palila fecal analysis indicated that palila did not consume pods or flowers more frequently within or outside of the breeding season (see Chapter 14: Diet), but further quantitative analysis may reveal seasonal variation in the daily volume of seeds and flowers in the diet.

We did not observe a seasonal progression of pod production from high to low elevation over our 7-year study, as was reported during a 10-year study (1992–2001) on the western slope (Banko *et al.* 2002a). Instead, pod production peaked in May–June at all elevations during 1998–2005. Whereas the overall peak in pod abundance at the higher elevations on the western slope was June during 1998–2005, pods peaked in January and were sustained at very high levels through April at high elevation during 1992–2001. A factor contributing to the recent high degree of fruiting synchronization along the elevation gradient may have been the drought that persisted during most of 1998–2005 (Banko *et al.* 2013). If true, then a trend toward drier conditions in subalpine Mauna Kea might lead to shorter breeding seasons for the

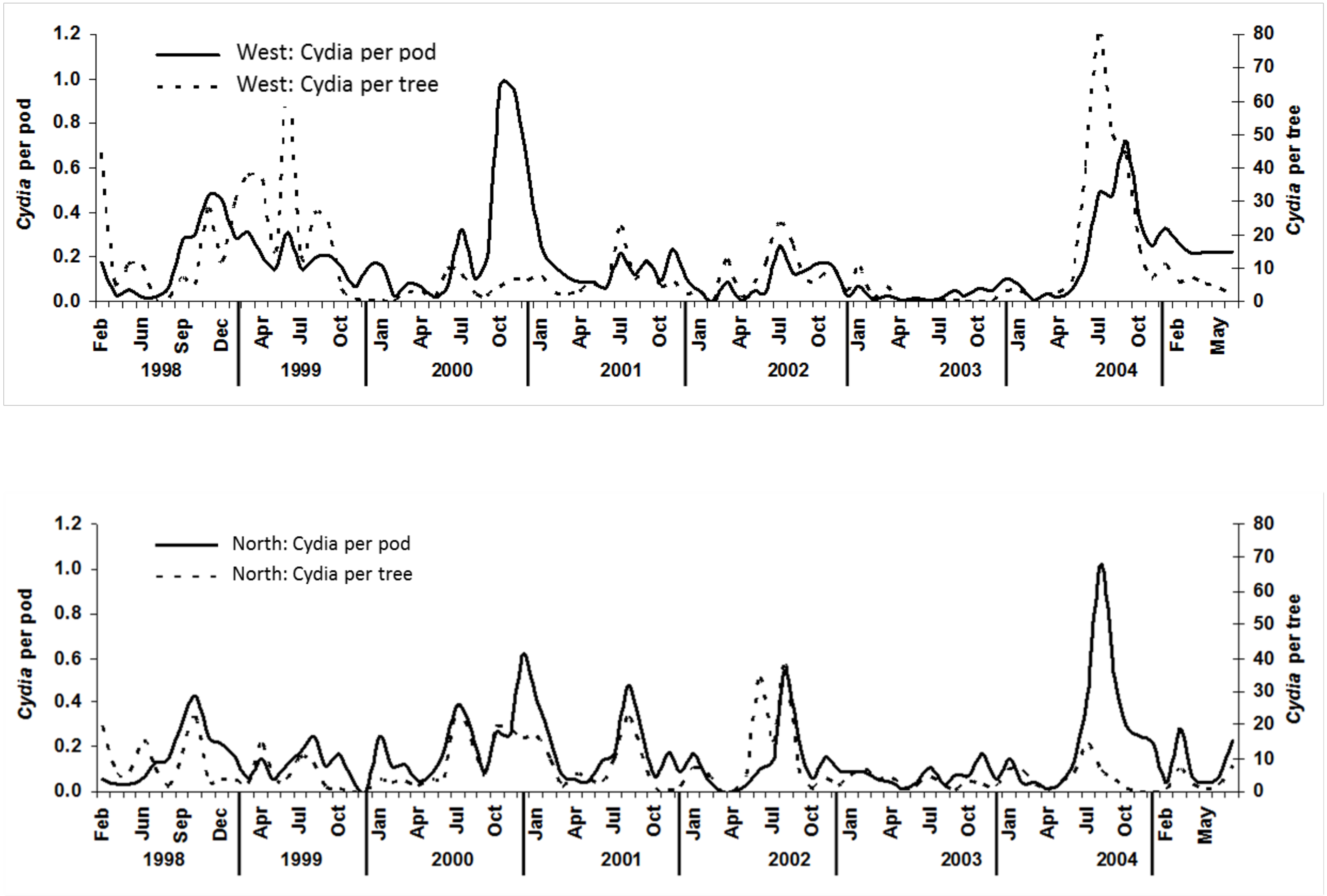
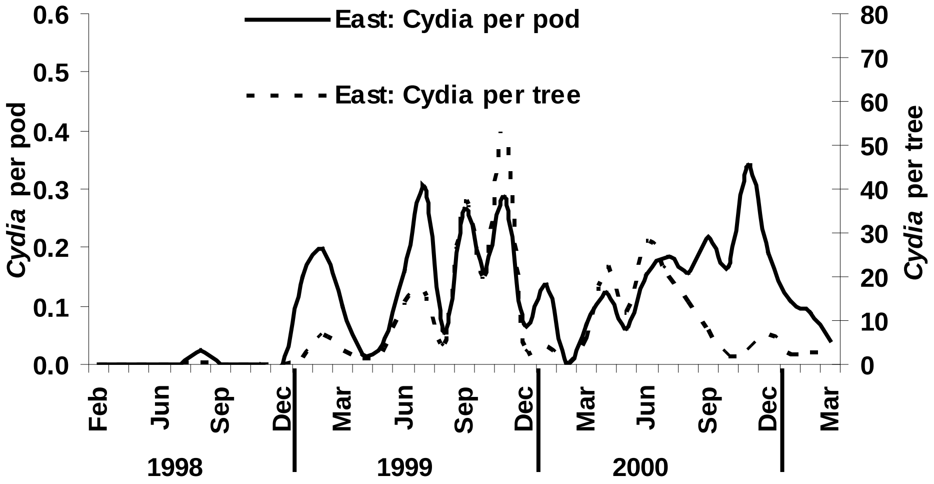


Figure 16.6. Average number of *Cydia* caterpillars per māmane pod and per tree on the four slopes of Mauna Kea from February 1998 to March 2001 (east and south) or June 2005 (west and north).



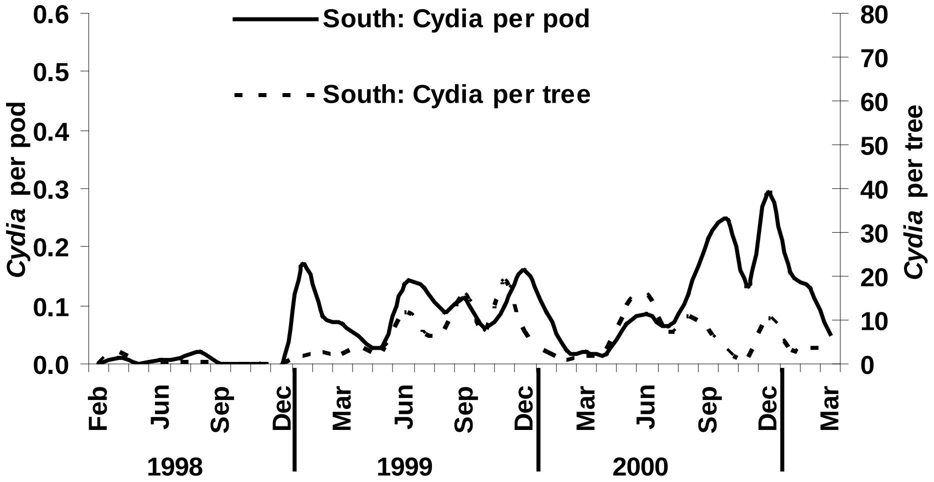


Figure 16.6 (continued). Average number of *Cydia* larvae per māmane pod and per tree on the four slopes of Mauna Kea from February 1998 to March 2001 (east and south) or June 2005 (west and north).

Table 16.2. Mean elapsed time between selected stages in the development of māmane pods.

Development period	Mean time (days)	*n*	90% confidence interval Lower	90% confidence interval Upper
Bud → flower	49.7	2,545	49.0	50.4
Flower → edible pod	98.1	715	96.4	99.9
Edible pod→ old pod	132.2	300	127.7	136.6

palila because pods would be abundant across the landscape for less time. Moreover, the size of pod crops is reduced by drought (Banko *et al.* 2013). Overall, the mean (± SE) number of pods per tree (111.9 ± 6.01) at high elevation on the western slope during 1998−2005 was half the amount (221.7 ± 9.97) recorded during 1992−2001.

The abundance of *Cydia* caterpillars was episodic in all areas of Mauna Kea. The number of *Cydia* per pod peaked in November when pods were relatively uncommon. Presumably as pods become less abundant, *Cydia* become more concentrated in the remaining pods. Nevertheless, the overall availability of caterpillars per tree was highest in June when pods were abundant and many palila were breeding (see Chapter 9: Breeding Phenology, Productivity, and Nesting Success). *Cydia* caterpillars were the most common insect food item consumed by palila (see Chapter 14: Diet) and were consistently available throughout the habitat occupied by the birds during our study.

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17 FOOD AVAILABILITY: FOLIAR CATERPILLARS

John W. Slotterback, Peter T. Oboyski, Paul C. Banko

Introduction

Māmane (*Sophora chrysophylla*) trees on Mauna Kea are host to foliar-feeding caterpillars. These caterpillars represent food resources to insect-eating birds such as palila (*Loxioides bailleui*) and Hawai‘i ‘amakihi (*Hemignathus virens*). Little is known of the species composition, distribution, and limiting factors of this guild of caterpillars. To learn more about foliar-feeding caterpillars on māmane, we conducted surveys on the western and northern slopes of Mauna Kea during 1999−2000.

Methods

We sampled caterpillars at stations along Hawai‘i Forest Bird Survey transects on the western and northern slopes of Mauna Kea, Hawai‘i (Figure 17.1). Samples were collected from March, April, and September–November in 1999; then again in March, September, and October in 2000. Collecting stations were grouped by 150-m elevation bands between 2,200–2,800 m elevations (Figure 17.1). We sampled at four stations at each elevation on each slope, yielding 20 samples per slope and 40 total samples for both slopes. Samples were taken between 0800 hours and 1600 hours on days with no heavy cloud cover or rain. Though other tree species were also sampled, only results from māmane trees are presented here.

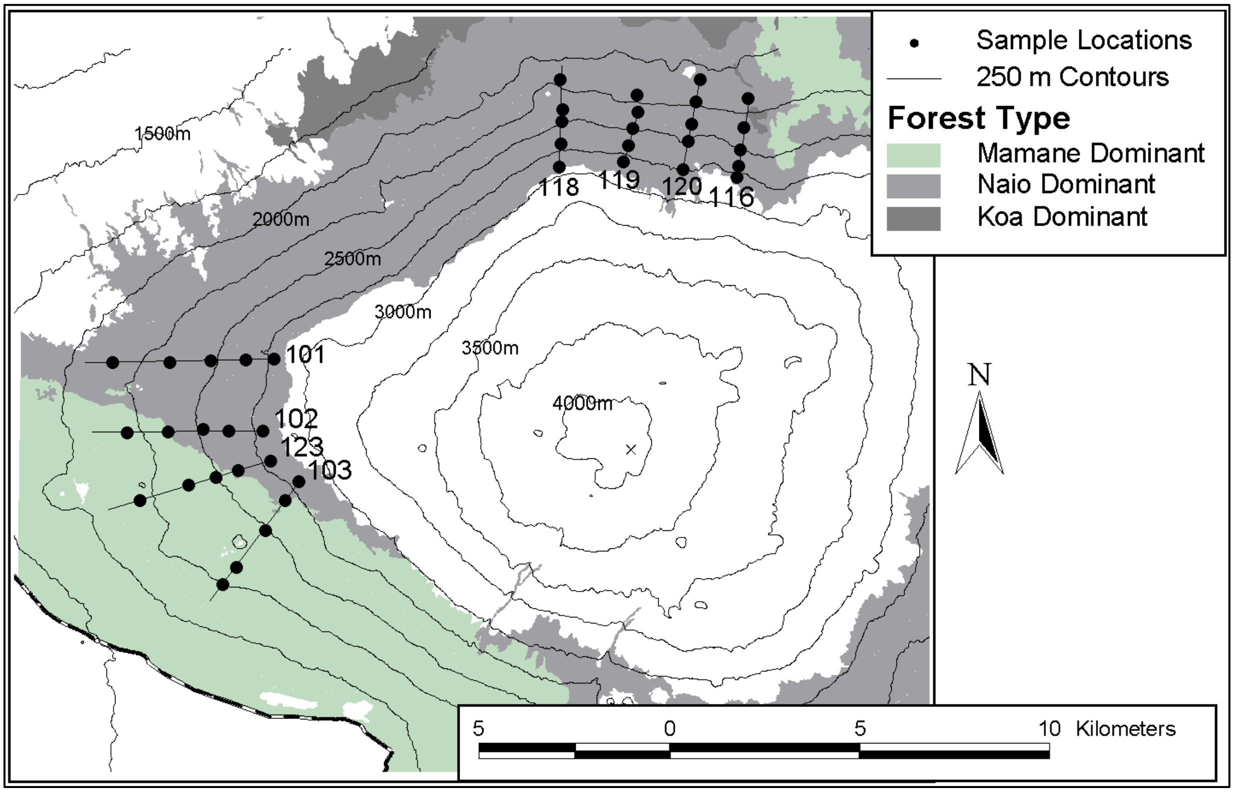

Figure 17.1. Foliar caterpillar sample locations along Hawai‘i Forest Bird Survey transects on western and northern slopes of Mauna Kea, Hawai‘i, during 1999–2000.

Caterpillars were collected at each station by shaking māmane branches vigorously over a 1-m^2 sheet. We sampled the branches of one or more trees within 100 m of the station until one minute had elapsed, then we inspected the sheet for caterpillars. We repeated this procedure up to seven times at each station, depending on tree availability, because preliminary sampling revealed that seven minutes was usually required to collect at least one caterpillar.

Caterpillars were stored alive in dry vials containing māmane leaves and kept cool until they could be transported to the laboratory at Kīlauea Field Station and transferred into individual rearing containers. Caterpillars were reared on māmane leaves in 240-ml containers fitted with screen covers in the laboratory until an adult moth or parasitoid emerged or until the caterpillar died. Information on parasitoid wasps and caterpillar mortality is reported elsewhere (see Chapter 20: Threats to Food Resources: Foliar Caterpillar Parasitism).

Results

Caterpillars were collected from all elevations on both slopes, but they were encountered most frequently at 2,650 m elevation and least frequently at 2,200 m (Table 17.1; Figures 17.2, 17.3). A total of 305 caterpillars were collected from the northern slope during 610 minutes of sampling over 10 days, and 109 caterpillars were collected from the western slope during 489 minutes of sampling spread over 11 days (Table 17.1). Of these, 76% were *Scotorythra artemidora* Zimmerman (Lepidoptera: Geometridae) and 23% were *Peridroma albiorbis* Warren (Lepidoptera: Noctuidae), whose host plant was previously unknown.

Table 17.1. Abundance of foliar caterpillars on the northern and western slopes of Mauna Kea, Hawai'i, 1999–2000. Total sampling time (minutes) is shown for each elevation (meters) and year.

Slope	Elev. (m)	Time (min.)		*Scotorythra artemidora*		*Peridroma albiorbis*		Total caterpillars
		1999	2000	1999	2000	1999	2000	
Northern	2,200	42	68	11	2	4	2	19
	2,350	35	81	41	3	2	1	47
	2,500	46	91	29	5	1	12	47
	2,650	42	82	83	5	5	11	104
	2,800	47	76	32	3	2	51	88
	All	212	398	196	18	14	77	305
Western	2,200	10	45	2	0	0	0	2
	2,350	37	81	26	0	0	0	26
	2,500	39	69	11	3	0	0	14
	2,650	47	56	40	3	2	3	48
	2,800	42	63	7	10	2	0	19
	All	175	314	86	16	4	3	109
Total	All	387	712	282	34	18	80	414

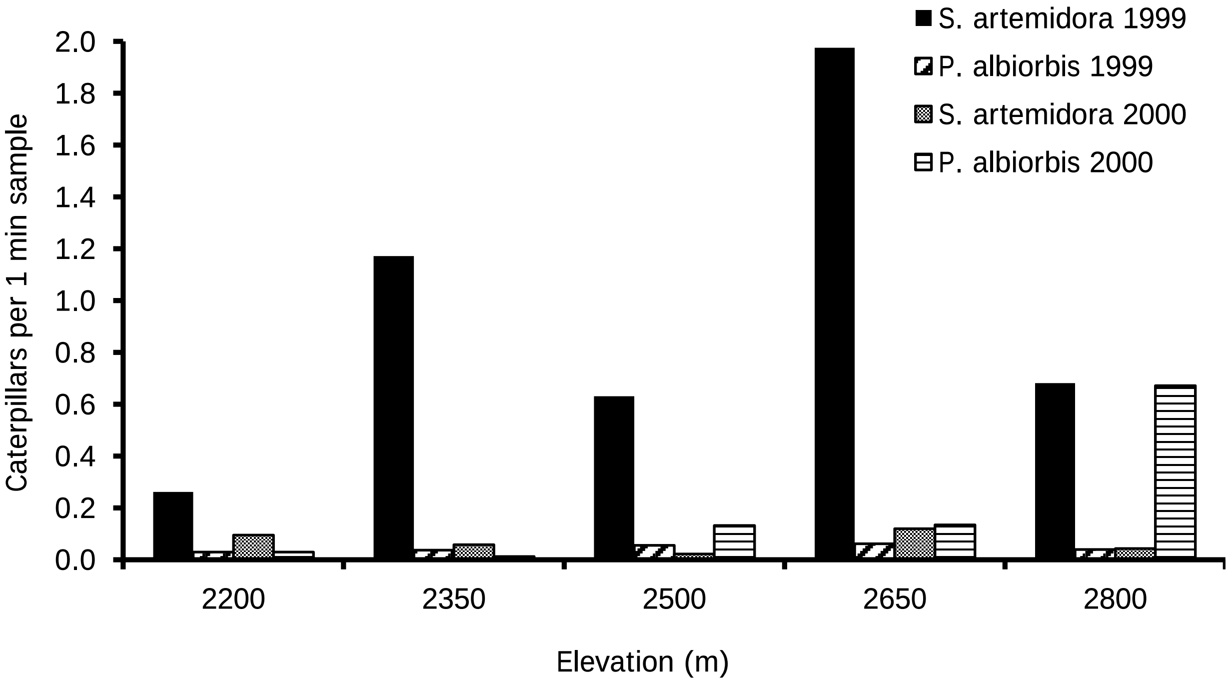

Figure 17.2. Relative abundance of *Scotorythra artemidora* and *Peridroma albiorbis* at different elevations on the northern slope of Mauna Kea, Hawai'i, 1999–2000.

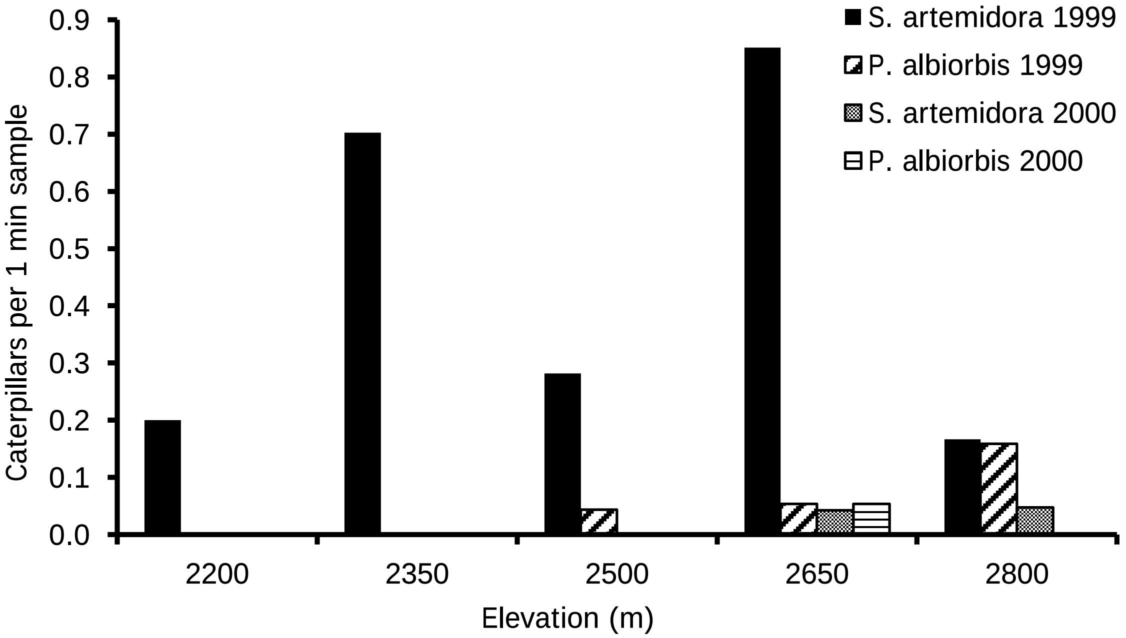

Figure 17.3. Relative abundance of *Scotorythra artemidora* and *Peridroma albiorbis* at different elevations on the western slope of Mauna Kea, Hawai'i, 1999–2000.

Scotorythra artemidora was the most abundant caterpillar taken in both years of the study and was more abundant in 1999 than in 2000 (Figures 17.2, 17.3). *P. albiorbis* was more abundant on the northern slope in 2000 than it was in 1999, and it was less abundant on the western slope during 2000 than it was in 1999 (Figures 17.2, 17.3).

Scotorythra caterpillars averaged less than 8 mm long at the time of collection, but reached nearly 40 mm as late instars (mature larvae). Of 414 caterpillars collected, less than seven percent were initially over 15 mm in length, which represented early instars (young larvae) for *Scotorythra* and *Peridroma*. *Scotorythra artemidora* caterpillars were usually pale to medium green with a white dorsal line when collected, but they often changed to a light tan color in the laboratory. A second color morph exhibited by this species was a medium-to-dark grey that did not change appreciably over time. *Peridroma* caterpillars exhibited several color patterns in various shades of brown. Other caterpillars were collected infrequently in our samples. Among these were *Uresiphita polygonalis virescens* (Butler; Crambidae), which was considered to be a major insect food of palila and māmane defoliator by Perkins (1903, 1913); *Thyrocopa indecora* (Butler; Oecophoridae), an endemic moth whose larvae feed beneath the bark of dead māmane limbs; and *Lampides boeticus* (Linnaeus; Lycaenidae), an adventive butterfly that feeds on a wide variety of leguminous plants.

Discussion

Scotorythra artemidora was the most abundant caterpillar taken in both years of the study, but it was collected much more frequently in 1999. Possible explanations for the variation in abundance of this māmane-associated species are small sample sizes, differences in microhabitats, variation in rainfall, and uneven timing of sampling during the year. Further work is needed to understand the life history and population dynamics of this poorly-known species.

The host plant for *Peridroma albiorbis* (Noctuidae) was previously unknown; we reared this species from both māmane and ʻāheahea (*Chenopodium oahuensis*; U.S. Geological Survey unpublished data). Because relatively little collecting has been done in māmane forests above 1,200 m elevation, it is not known how prevalent these caterpillars may have been historically. Perkins (1913) noted that the caterpillars of some *Scotorythra* species are nocturnal feeders. Early instars can sometimes be found feeding during the day while later instars spend daylight hours in seclusion and feed at night (M. Heddle, University of California at Berkeley, personal communication). Virtually all caterpillars collected in this study were early instars, therefore our daytime sampling was likely biased against older, larger caterpillars. Nevertheless, our sampling took place during the hours when birds would be most actively foraging, which realistically reflects food availability for palila and other species.

Perkins (1913) also observed that "[*Scotorythra*] form a most important part of the food supply of endemic birds, and are supplied by the parents to the young of nearly all the species..." In reference to palila, he remarked that "it feeds its young on caterpillars, and is itself at some seasons most partial to such food, a considerable variety of these being found in its stomach." Recent studies (see Chapter 14: Diet) revealed that caterpillar parts of species other than *Cydia* were not found frequently in palila fecal samples collected above 2,200 m elevation. This suggests that the palila we investigated on the western slope of Mauna Kea consumed fewer foliar caterpillars than did palila collected by Perkins a century earlier at lower elevation (1,220−1,525 m) on the western slope of Mauna Loa (Banko 1979).

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18 FOOD AVAILABILITY: INSECT SURVEYS IN THE PU‘U MALI MITIGATION PARCEL

David Pollock, Paul C. Banko

Introduction

Native forest restoration on the pasturelands near Pu‘u Mali on the northern slope of Mauna Kea will partially mitigate the loss of critical habitat for palila (*Loxioides bailleui*) due to the realignment of Saddle Road (Highway 200) on the southern slope of Mauna Kea (U.S. Fish and Wildlife Service 1998, Federal Highway Administration 1999). We surveyed Lepidoptera and Hymenoptera in the mitigation parcel during 2004–2005 to support the reintroduction of palila to the northern slope and provide data for future assessments of forest and ecosystem restoration.

Both Lepidoptera and Hymenoptera figure prominently in the feeding ecology of the palila. Palila supplement their diet of māmane (*Sophora chrysophylla*) seeds by feeding on *Cydia* caterpillars, which also feed on māmane seeds, and by foraging for other Lepidoptera larvae on vegetation (Banko *et al*. 2002a). Some Hymenoptera attack or parasitize Lepidoptera larvae, which may have an impact on the availability of the palila’s food resources (Banko *et al*. 2002b, Brenner *et al*. 2002; see Chapter 19: Threats to Food Resources: *Cydia* Caterpillar Parasitism and Chapter 20: Threats to Food Resources: Foliar Caterpillar Parasitism). For example, large populations of ants (Formicidae) are able to drastically reduce populations of native insects that are part of young birds’ diets (Cole *et al.* 1992). Parasitic Hymenoptera also have the potential to reduce the availability of Lepidoptera prey. Brenner *et al*. (2002) found that at some sites on Mauna Kea, 90% of *Cydia* caterpillars were parasitized. The Ichneumonidae and Braconidae are of particular concern since they include many species that parasitize Lepidoptera.

Methods

Lepidoptera Collection

Adult Lepidoptera were surveyed primarily with blacklight traps. Each trap consisted of a 3.5 gallon polypropylene bucket with an aluminum funnel and lid, four-way bungee cord assembly, rain drain, three-part clear acrylic vane, and 22-watt Circline blacklight tube with ballast cord and photoelectric switch. The trap was powered by a 12-volt DC lead-acid battery pack with fully jelled electrolyte to prevent leakage. The killing agent was ethyl acetate. Vaseline was spread around the top and drain opening to prevent ants from entering the trap. We placed a total of 17 blacklight traps in a variety of habitat types in the Pu‘u Mali mitigation parcel for five nights during May–July 2004 (Figure 18.1, Table 18.1). Traps were operated from dusk until the battery power was drained (approximately six hours).

On four dates, Lepidoptera were hand-collected at a white sheet that was hung between two trees (Figure 18.1, Table 18.1). The sheet was illuminated with a 22-watt blacklight. This collection method allowed us to selectively obtain specimens for preservation. Specimens were usually in better condition than those collected in a blacklight trap. Presence or absence of species was noted during sheet-collecting events. Sheet-collecting was usually conducted during the first few hours after dusk.

Finally, some specimens were collected with aerial nets during four general collecting sessions (Figure 18.1, Table 18.1). This method relied on visual identification of insects before collection occurred. All specimens were kept alive until returned to the lab, where they were placed in a

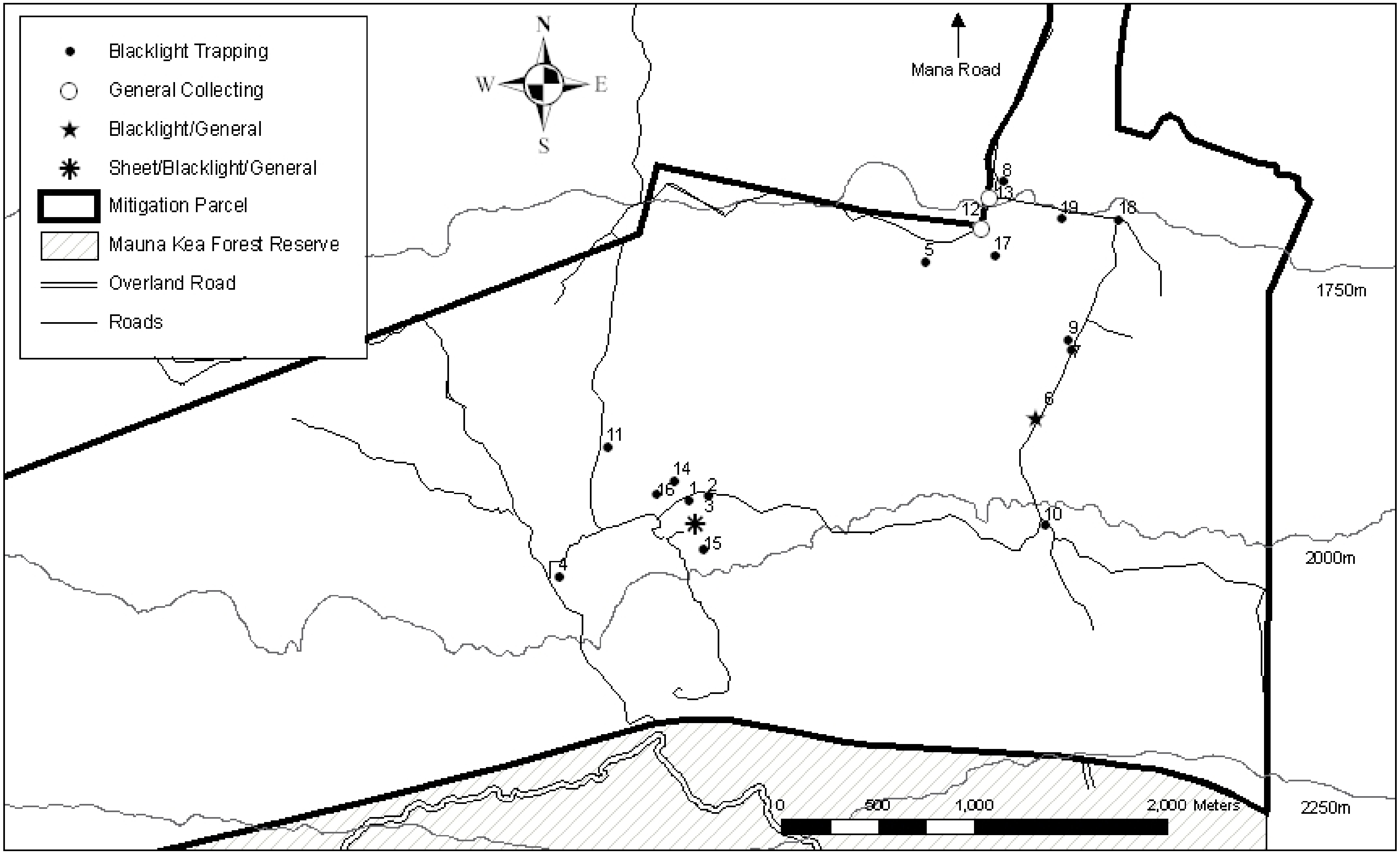

Figure 18.1. Lepidoptera collection locations in the Pu‘u Mali mitigation parcel, northern slope of Mauna Kea, May–July 2004.

Table 18.1. Lepidoptera collection methods and dates in the Puʻu Mali mitigation parcel, northern slope of Mauna Kea, 2004. Location numbers refer to Figure 18.1.

Collection method	Location	Date
Blacklight trap	1	4 May
Blacklight trap	2	4 May
Blacklight trap	4	14 June
Blacklight trap	5	14 June
Blacklight trap	6	14 June
Blacklight trap	7	14 June
Blacklight trap	8	15 June
Blacklight trap	9	15 June
Blacklight trap	10	15 June
Blacklight trap	11	15 June
Blacklight trap	3	14 July
Blacklight trap	14	14 July
Blacklight trap	15	14 July
Blacklight trap	16	21 July
Blacklight trap	17	21 July
Blacklight trap	18	21 July
Blacklight trap	19	21 July
Sheet	3	4 May
Sheet	3	13 July
Sheet	3	19 July
Sheet	3	20 July
General collecting	3	4 May
General collecting	3	5 May
General collecting	12	15 June
General collecting	6	16 June
General collecting	13	16 June

freezer. This method allowed us to catch species that might not be caught with other traps and allowed targeted collection at non-random sites.

Additional blacklight trapping, sheet-collecting, and general collecting were conducted from August 2004 until June 2005. These specimens remain unidentified.

Approximately 100 Lepidoptera larvae were collected from māmane in the Puʻu Mali area on 1 July 2005 during three hours of collection. A 71-cm^2 canvas supported by a wooden frame was placed under a tree while a wooden stick was used to beat the vegetation immediately above the canvas. The larvae were raised in the laboratory to determine their species identity, life history, and parasitism rates (U.S. Geological Survey unpublished data).

Hymenoptera Collection

Hymenoptera were collected using a combination of yellow pan traps and malaise traps. Pan traps were yellow plastic bowls with a 15-cm diameter and a depth of 4.3 cm, containing approximately 250 ml of soapy water. Trap stations were located at 600-m intervals along Hawaiʻi Forest Bird Survey (HFBS) transects (Figure 18.2). At each station, we placed four

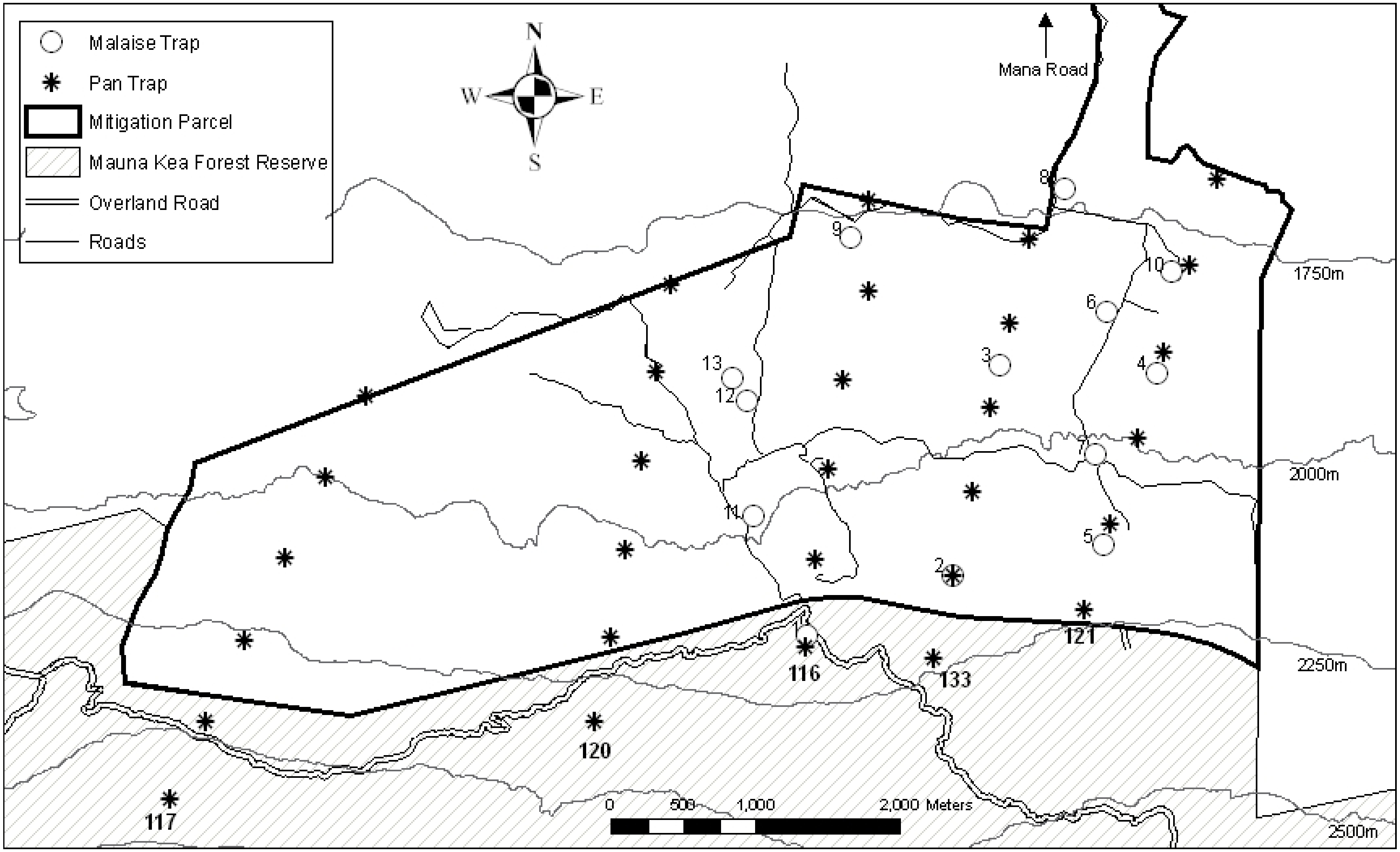

Figure 18.2. Location of pan and malaise traps in the Pu'u Mali mitigation parcel, northern slope of Mauna Kea, 2004–2005. Hawai'i Forest Bird Survey transects surveyed were 117, 120, 116, 133, and 121. Malaise traps are numbered 1–13.

traps approximately 10 m from the station tag. The traps were left in the field for three days during each month of collecting (Table 18.2). Contents from the four traps were combined and identified in the lab.

Table 18.2. Summary of collecting dates for pan traps in the Pu‘u Mali mitigation parcel, northern slope of Mauna Kea, 2004–2005.

Transect	Sept 04	Oct 04	Nov 04	Dec 04	Jan 05	Feb 05	Mar 05
116	X		X		X	X	X
117		X					
120		X					X
121	X	X	X	X	X	X	X
133	X	X	X	X	X	X	X

Malaise traps were flight-interception devices made of green polyester netting, with a collecting head containing 50% antifreeze (Townes 1972). We operated malaise traps during July 2004–March 2005 (Figure 18.2, Table 18.3), but traps were not run continuously during this period due to high winds and cattle damage. In July and August 2005, we set up eight traps in representative habitat types (MAL 6–13), and in October 2005, we set up an additional five traps (MAL 1–5) along transects 116, 133, and 121 (Figure 18.2). We did not set up malaise traps on the remaining transects because of cattle presence. Trap heads were removed monthly to retrieve the catch. Hymenoptera from pan and malaise traps were identified to family, and when possible, to the species level.

Table 18.3. Summary of collecting dates (month and year) for malaise traps in the Pu‘u Mali mitigation parcel, northern slope of Mauna Kea, 2004–2005.

Malaise trap	Jul 04	Aug 04	Sep 04	Oct 04	Nov 04	Dec 04	Jan 05	Feb 05	Mar 05
MAL 1				X	X	X	X	X	X
MAL 2				X	X	X	X	X	X
MAL 3				X	X	X	X	X	X
MAL 4				X	X	X	X	X	X
MAL 5				X	X	X	X	X	X
MAL 6	X	X	X	X	X	X	X	X	X
MAL 7	X	X	X	X	X	X	X	X	X
MAL 8	X		X	X	X	X	X		X
MAL 9		X	X	X	X				
MAL 10	X	X	X	X	X		X		
MAL 11				X		X	X	X	X
MAL 12	X								
MAL 13		X							

Six HFBS transects in the Pu‘u Mali mitigation parcel were surveyed for ants during 27–28 October 2005 (Figure 18.3). We also conducted some initial pilot surveys in the central portion of the mitigation lands that were not along the transects on 13–15 September 2005 (*n* = 44 stations) and 13 October 2005 (*n* = 38 stations). Stations were located at 200-m intervals along the transects. We baited clear plastic lids (approximately 5 cm in diameter) with a drop of honey and tuna, and then placed three lids within 5 m of each station. After two to four hours we estimated the number of ants on each lid and collected representative specimens into 70% ethanol.

Results

Lepidoptera

In all, 42 species, including 22 endemic species, from 14 families of Lepidoptera were collected (Table 18.4). Eighty-one caterpillars of *Uresiphita polygonalis* (Denis & Schiffermüeller) and one other species were successfully transported to the lab. As of 15 August 2005, when rearing activities were terminated, 12 caterpillars had died of unknown causes (including the single unidentified non-*Uresiphita*), and six had emerged successfully as moths. Two *Diadegma blackburni* Cameron parasitoids had also emerged.

Parasitic Hymenoptera

We collected 2,621 specimens from 28 families of Hymenoptera in pan traps (Table 18.5). Of these, 20 families (85%, 2,226 specimens) are generally parasitic on other arthropods. Representatives from the Mymaridae, Encyrtidae, and Eulophidae were by far the most abundant parasitoids, consisting of 56% (1,245/2,226 specimens) of the total number of parasitic Hymenoptera. We collected 124 Ichneumonidae, about half of which were *Diadegma blackburni*. The pan traps also collected 337 Braconidae, nearly half of which were of the subfamily Aphidiinae, and 7 additional subfamilies made up the remainder.

The malaise traps collected over 2,966 Hymenoptera from 21 families (Table 18.5), 15 of which are generally parasitic (2,672 specimens). Ichneumonidae made up 89% of the parasitoids collected. *Diadegma blackburni* was again the most abundant ichneumonid wasp. One hundred and fifty-six Braconidae were collected; 42% of these were *Meteorus laphygmae*.

Ants

Although ants were collected incidentally in both pan and malaise traps, the intensive ant survey provided detailed information on the distribution of ants in the Pu‘u Mali mitigation parcel (Figure 18.3). Two species of ant were collected: Argentine ant (*Linepithema humile* Mayr) and *Cardiocondyla kagutsuchi* Terayama. Both are accidentally introduced species that pose major threats to the fauna of the mitigation lands (see Chapter 22: Threats to Food Resources: Ants). The Argentine ant was dominant in the northeastern corner of the mitigation parcel, extending from the northern limit of the parcel to a maximum elevation of approximately 2,100 m. A second population of *L. humile* was found in the center of the Pu‘u Mali mitigation parcel (labeled A in Figure 18.3). The distribution of *C. kagutsuchi* was more scattered with its highest concentration near HFBS transect 116, slightly below 2,000 m.

Other Hymenoptera

Other major hymenopteran threats to the fauna of the mitigation lands included the predaceous western yellowjacket (*Vespula pensylvanica*; see Chapter 21: Threats to Food Resources: Yellowjackets) and at least one species of *Polistes* paper wasp (Table 18.5). A total of 12 *V. pensylvanica* were collected in pan traps, while malaise traps collected 31 specimens. *Polistes*

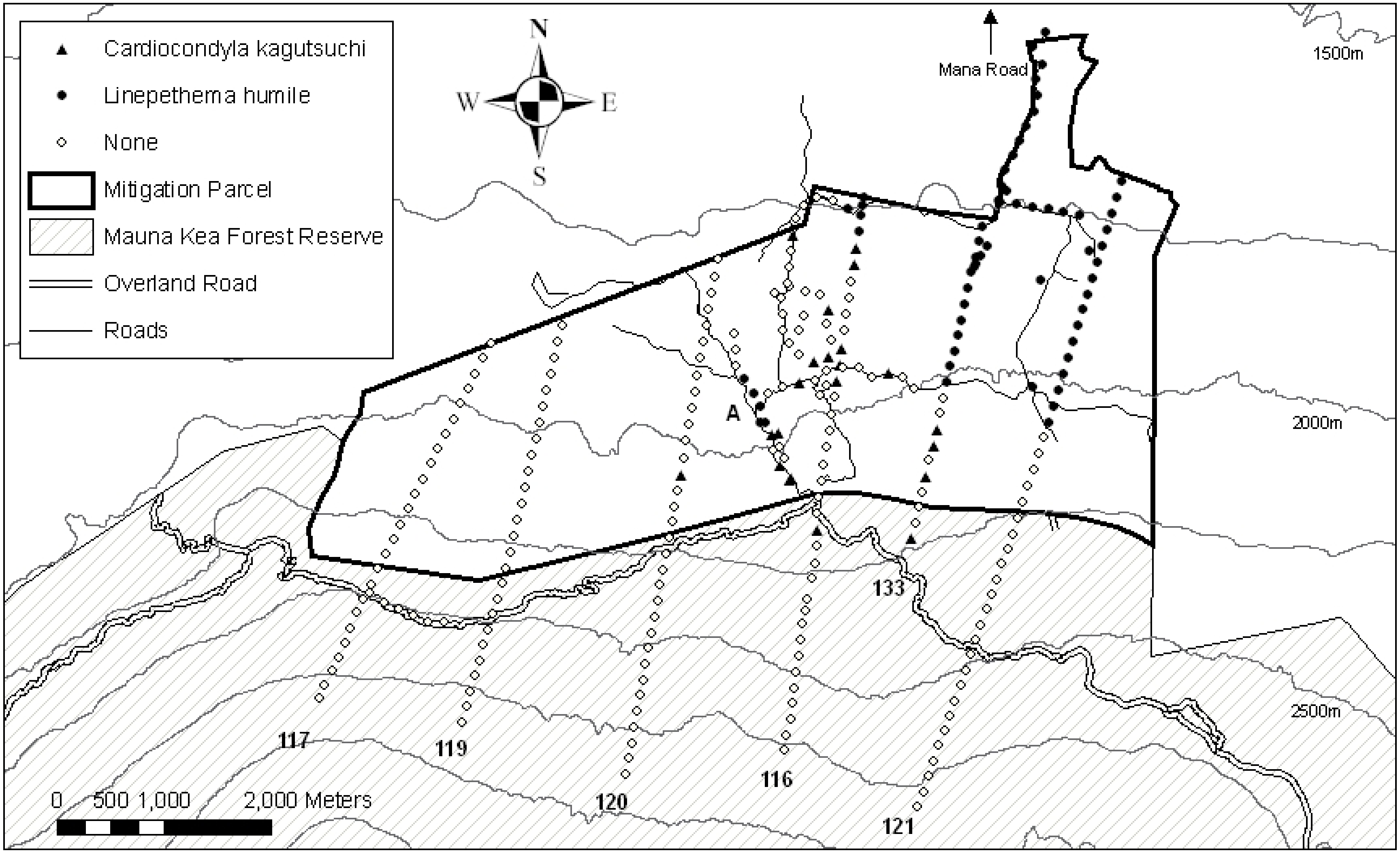

Figure 18.3. Distribution of *Cardiocondyla kagutsuchi* and *Linepithema humile* in the Pu'u Mali mitigation parcel, northern slope of Mauna Kea, 2005. Hawai'i Forest Bird Survey transects surveyed were 117, 119, 120, 116, 133, and 121. "A" marks a smaller, disjunct population of *L. humile*.

Table 18.4. Lepidoptera collected in the Puʻu Mali mitigation parcel, May–July 2004.

Family	Species	Status[1]
Carposinidae	*Carposina gracillima* (Walsingham)	End
Cosmopterigidae	*Hyposmocoma* sp. 1	End
Cosmopterigidae	*Hyposmocoma* sp. 2	End
Crambidae	*Eudonia actias* (Meyrick)	End
Crambidae	*Eudonia melichlora* (Meyrick)	End
Crambidae	*Eudonia* sp. 1	End
Crambidae	*Eudonia* sp. 2	End
Crambidae	*Eudonia* sp. 3	End
Crambidae	*Eudonia* sp. 4	End
Crambidae	*Eudonia* sp. 5	End
Crambidae	*Eudonia* sp. 6	End
Crambidae	*Eudonia* sp. 7	End
Crambidae	*Eudonia* sp. 8	End
Crambidae	*Nomophila noctuella* (Denis & Schiffermüeller)	Acc
Crambidae	*Omiodes accepta* (Butler)	End
Crambidae	*Omiodes continuatalis* (Wallengren)	End
Crambidae	*Spoladea recurvalis* (Fabricius)	Acc
Crambidae	*Uresiphita polygonalis* (Denis & Schiffermüeller)	Acc
Hesperiidae	*Hylephila phyleus* (Drury)	Acc
Lycaenidae	*Lampides boeticus* (Linnaeus)	Acc
Noctuidae	*Ascalapha odorata* (Linnaeus)	Acc
Noctuidae	*Agrotis dislocata* (Walker)	End
Noctuidae	*Agrotis melanoneura* Meyrick	End
Noctuidae	*Athetis thoracica* (Moore)	Acc
Noctuidae	*Autographa biloba* (Stephens)	Acc
Noctuidae	*Lycophotia porphyrea* (Denis & Schiffermüeller)	Acc
Noctuidae	*Pseudaletia unipuncta* (Haworth)	Acc
Noctuidae	*Pseudaletia* sp. new	End
Noctuidae	*Schrankia* sp. 1	End
Nymphalidae	*Danaus plexippus* (Linnaeus)	Acc
Nymphalidae	*Vanessa atalanta* (Linnaeus)	Acc
Nymphalidae	*Vanessa virginiensis* (Drury)	Acc
Oecophoridae	*Thyrocopa indecora* (Butler)	End
Pieridae	*Pieris rapae* (Linnaeus)	Acc
Pterophoridae	*Stenoptilodes* sp. 1	Acc
Pterophoridae	*Stenoptilodes* sp. 2	Acc
Plutellidae	*Plutella* sp. 1	Acc
Pyralidae	Pyralid sp. 1	Acc
Sphingidae	*Hyles wilsoni* (Rothschild)	End
Tortricidae	*Cryptophlebia illepida* (Butler)	Acc
Tortricidae	*Cydia* sp. 1	End
Tortricidae	Tortricid sp. 1	Acc

[1] Status: Acc = Accidentally introduced; End = Endemic (Nishida 2002)

Table 18.5. Families and species of Hymenoptera collected from pan and malaise traps in the Puʻu Mali mitigation parcel, northern slope of Mauna Kea, July 2004–March 2005.

Taxa	Status[1]	Guild[2]	Host[3]	Pan	Malaise
Agaonidae	Intro	Phyto	n/a	3	0
Aphelinidae	Intro	Ptoid	**Ho,***Le,Or,Di, Hy*	41	1
Apidae					
Apis mellifera Linnaeus	Pur	Poll	n/a	38	16
Bethylidae					
Sierola? sp. A	End?	Ptoid	**Le**	6	0
Sierola? sp. B	End?	Ptoid	**Le**	2	0
Sierola? sp. C	End?	Ptoid	**Le**	0	1
Braconidae					
Alysiinae					
Aphaereta pallipes Say	Acc	Ptoid	**Di**	3	6
Aspilota sp. A	End?	Ptoid	**Di**	10	0
Aspilota konae Ashmead	End	Ptoid	**Di**	2	0
Aphidiinae					
Aphidius smithi Sharma & Subba Rao	Pur	Ptoid	**Ho**	24	5
Aphidius sp.	Intro	Ptoid	**Ho**	1	6
Diaeretiella rapae (M'Intosh)	Acc	Ptoid	**Ho**	71	0
Lysiphlebius testaceipes (Cresson)	Pur	Ptoid	**Ho**	1	0
?*Monoctonus nervosus* (Haliday)	Intro	Ptoid	**Ho**	14	2
Aphidiinae sp. A	Intro	Ptoid	**Ho**	163	19
Aphidiinae sp. E	Intro	Ptoid	**Ho**	1	0
Blacinae					
Blacus sp.	Acc	Ptoid	**Le/Co**	2	0
Meteorinae					
Meteorus laphygmae Cresson	Pur	Ptoid	**Le**	3	72
Opiinae					
Opius lantanae Bridwell	Acc	Ptoid	**Di**	4	0
Orgilinae					
Orgilus swezeyi Fullaway	Acc	Ptoid	**Le**	7	11
Doryctinae					
Rhaconotus vagrans (Bridwell)	Acc	Ptoid	**Co**	2	3
Euphorinae					
Euphorinae sp. A	Intro	Ptoid	**In**	0	1
Microgastrinae					
Microgastrinae sp. A	Intro	Ptoid	**Le**	1	2
Microgastrinae sp. B	Intro	Ptoid	**Le**	0	2
Microgastrinae sp. D	Intro	Ptoid	**Le**	1	6
Microgastrinae sp. E	Intro	Ptoid	**Le**	0	1
Microgastrinae sp. F	Intro	Ptoid	**Le**	0	1
Microgastrinae sp. G	Intro	Ptoid	**Le**	19	7
Microgastrinae sp. H	Intro	Ptoid	**Le**	1	7
Microgastrinae sp. J	Intro	Ptoid	**Le**	1	0

Table 18.5 (continued).

Taxa	Status[1]	Guild[2]	Host[3]	Pan	Malaise
Braconidae sp. B	?	Ptoid	**?**	1	0
Ceraphronidae	Acc	Ptoid	**In**	5	0
Chalcididae	Intro	Ptoid	**Le,Di,***Hy,Co*	0	3
Colletidae					
Hylaeus spp. (♀)	End	Poll	n/a	15	4
Hylaeus sp. A (♂)	End	Poll	n/a	2	1
Hylaeus sp. B (♂)	End	Poll	n/a	1	0
Hylaeus sp. C (♂)	End	Poll	n/a	1	0
Hylaeus sp. E (♂)	End	Poll	n/a	0	1
Hylaeus sp. F (♂)	End	Poll	n/a	0	2
Hylaeus sp. I (♂)	End	Poll	n/a	1	0
Diapriidae	Mult	Ptoid	**Di,***Co,Hy*	8	0
Encyrtidae	Mult	Ptoid	**Ho,***In*	395	7
Eulophidae	Mult	Ptoid	**Le,Di,Hy, Co,***In*	387	14
Eupelmidae	Mult	Ptoid	**In**	3	2
Figitidae					
Charipinae	Acc	Ptoid	**Hy**	29	6
Eucoilinae	Mult	Ptoid	**Di**	15	0
Formicidae					
Cardiocondyla kagatsuchi	Acc	Omni	n/a	5	0
Linepithema humile Mayr	Acc	Omni	n/a	300	212+
Heloridae					
Helorus ruficornis Förster	Acc	Ptoid	**Ne**	1	10
Ichneumonidae					
Campopleginae					
Eriborus sinicus (Holmgren)	Pur	Ptoid	**Le**	0	1
Cremastinae					
Pristomerus hawaiiensis Perkins	End?	Ptoid	**Le**	1	48
Trathala flavoorbitalis Cameron	Acc	Ptoid	**Le**	1	1
Cryptinae					
Agasthenes swezeyi Cushman	Acc	Ptoid	**Ar**	11	16
Diplazontinae					
Diplazon laetatorius Fabricius	Acc	Ptoid	**Di**	1	92
Ephialtinae					
Calliephialtes graptolithae Cresson	Acc	Ptoid	**Le**	4	63
Gelinae					
Gelis tenellus (Thomson)	Acc	Ptoid	**Hy**	0	3
Mesostenus gracilis (Cresson)	Acc	Ptoid	**Le**	0	2
Ichneumoninae					
Barichneumon californicum Heinrich	Acc	Ptoid	**Le**	0	1
Ichneumon purpuripennis Cresson	Pur	Ptoid	**Le**	0	1
Ichneumon sp.	Intro	Ptoid	**Le**	1	5

Table 18.5 (continued).

Taxa	Status[1]	Guild[2]	Host[3]	Pan	Malaise
Rubicundiella perturbatrix Heinrich	Intro	Ptoid	**Le**	18	44
Spilichneumon superbus (Provancher)	Pur	Ptoid	**Le**	0	7
Metopiinae					
Hypsicera femoralis Fourcroy	Acc	Ptoid	**Le**	15	7
Pimplinae					
Pimpla punicipes Cresson	Acc	Ptoid	**Le**	3	34
Porizontinae					
Diadegma blackburni Cameron	End?	Ptoid	**Le**	66	1730
Diadegma insularis (Cresson)	Acc	Ptoid	**Le**	0	10
Diadegma pattoni Ashmead	Acc	Ptoid	**Le**	2	312
Hyposoter exiguae Viereck	Acc	Ptoid	**Le**	1	18
Megaspilidae	Acc	Ptoid	**In**	55	0
Mymaridae	Mult	Ptoid	**Ho,He,** *Ps, Co,Or,Di*	463	6
Platygastridae	Intro	Ptoid	**Di,** *Co,Ho*	19	0
Pompilidae					
Pompilinae	Acc	Ptoid	**Ar**	7	22
Ceropalinae	Acc	Ptoid	**Ar**	1	0
Proctotrupidae	Acc	Ptoid	**Co,** *Di*	50	25
Pteromalidae	Mult	Ptoid	**In**	20	15
Scelionidae					
Baeus sp.	Intro	Ptoid	**Ar**	86	0
Scelionidae spp.	Mult	Ptoid	**In,Ar**	145	13
Signiphoridae	Intro	Ptoid	**Ho,Hy,Di**	12	0
Sphecidae					
Crabroninae	Mult	Pred	n/a	2	16
Ectemnius polynesialis Cameron	End	Pred	n/a	5	4
Torymidae	Acc	Ptoid	Gall-forming **In**	4	1
Trichogrammatidae	Mult	Ptoid	**In**	16	0
Vespidae					
Eumeninae	Mult	Pred	n/a	5	3
Polistes spp.	Acc	Pred	n/a	3	2
Vespula pensylvanica Saussure	Acc	Pred	n/a	12	31
Total				2621	2966+

[1] Status: Acc = Accidentally introduced; End = Endemic; Intro = Introduced (unknown origin); Mult = Multiple status (i.e., some species are endemic, others are introduced); Pur = Purposely introduced; ? = Unknown (Nishida 2002)

[2] Guild: Omni = Omnivore; Phyto = Phytophagous; Poll = Pollinator; Pred = Predator; Ptoid = Parasitoid (Goulet and Huber 1993)

[3] Host: **Primary host(s),** *Secondary/less common host(s)*; In = Various Insecta; Co = Coleoptera; Di = Diptera; He = Hemiptera; Ho = Homoptera; Hy = Hymenoptera; Le = Lepidoptera; Ne = Neuroptera; Or = Orthoptera; Ps = Psocoptera; Th = Thysanura; Ar = Araneae (Swezey 1929, Townes 1947, Askew 1971, Goulet and Huber 1993, Beardsley 2000)

was less commonly collected (Table 18.5). Native Hymenoptera collected include approximately six species of *Hylaeus* (Colletidae) and *Ectemnius polynesialis* (Sphecidae; Table 18.5).

Discussion

Lepidoptera

The list of Lepidoptera from the Puʻu Mali mitigation parcel is preliminary. More species would likely be identified from the remaining specimens if the project were to be continued.

Species of note were *Omiodes continuatalis* (Wallengren), *Agrotis melanoneura* Meyrick, and *Pseudaletia* sp. new. *Omiodes continuatalis* was considered to be extinct since 1958, and *A. melanoneura* was thought to be possibly extinct (Hawaii Biological Survey 1999). *Pseudaletia* sp. new is an undescribed species of *Pseudaletia* that has been collected over a wide range on the island of Hawaiʻi. Voucher specimens for these species were submitted to the University of Hawaiʻi at Mānoa and Mississippi State University since Bishop Museum was not accepting arthropod specimens at the time.

The Lepidoptera larvae collected were almost all *Uresiphita polygonalis*. This species prefers māmane, where it was observed feeding heavily on māmane and being eaten by palila (Perkins 1903, 1913). Although it was originally believed to be endemic, Zimmerman and Hardy (1958) concluded that it was an introduced species. It is unsurprising that the two parasitoids emerging from *Uresiphita polygonalis* during the brief rearing trials were *Diadegma blackburni*, the most abundant ichneumonid in the Puʻu Mali mitigation parcel (see Parasitic Hymenoptera, below), but no conclusions can be inferred about parasitism rates from this limited sample.

Parasitic Hymenoptera

We collected 23 families of parasitic Hymenoptera, nine of which are not represented by any native species in Hawaiʻi. The Bethylidae collected were most likely *Sierola*, an extremely diverse genus endemic to Hawaiʻi. The remaining 13 families contained both native and non-native species. Therefore, we only classified specimens as native or non-native for those groups that we identified beyond family, specifically the Ichneumonidae and Braconidae.

The most abundant families collected were the Mymaridae, Encyrtidae, Eulophidae, Ichneumonidae, and Braconidae. Mymarids, or fairy-flies, are egg-parasites, particularly of Homoptera and Hemiptera (Askew 1971, Goulet and Huber 1993). Encyrtids are extremely diverse in Hawaiʻi, and are represented by a wide variety of both endemic and introduced species (Nishida 2002). They are typically parasitoids of Homoptera, particularly scale insects, though some species attack other orders, including Lepidoptera (Askew 1971). Many Eulophidae specialize on Lepidoptera larvae, although several other groups are also attacked (Goulet and Huber 1993). Most species of eulophids are introduced to Hawaiʻi, but a few are endemic (Nishida 2002). The wide variety of host preferences and the mix of endemic and introduced species in these and several other families collected emphasize the need to identify specimens to genus or preferably species level in order to determine their potential impacts on native arthropod communities.

Most of the Ichneumonidae collected parasitize Lepidoptera and, therefore, could be affecting palila food resources. The exceptions are *Agasthenes swezeyi*, which parasitizes spider eggs; *Diplazon laetatorius*, which parasitizes Syrphidae larva (Diptera); and *Gelis tenellus*, which is a hyperparasitoid of Braconidae, Ichneumonidae, and Chrysopidae cocoons (Swezey 1929, Beardsley 2000).

Diadegma blackburni may be native to Hawaiʽi, but (see Nishida 2002) only one specimen, which is suspect, has been reported elsewhere (Fullaway and Krauss 1945, Oboyski *et al*. 2004; J. Beardsley, University of Hawaiʽi at Mānoa, personal communication). *D. blackburni* has been reared from both concealed larvae (*Cydia* spp.) and exposed foliage-feeding caterpillars (e.g., *Scotorythra* sp.), on Mauna Kea (see Chapter 19: Threats to Food Resources: *Cydia* Caterpillar Parasitism and Chapter 20: Threats to Food Resources: Foliar Caterpillar Parasitism). Another potentially endemic ichneumonid is *Pristomerus hawaiiensis*, which was collected regularly, though not in large numbers. *P. hawaiiensis* was commonly reared from *Cydia* larvae on the western slope of Mauna Kea (see Chapter 19: Threats to Food Resources: *Cydia* Caterpillar Parasitism). Knowing the origins of both of these species would contribute greatly to understanding the interactions among māmane, *Cydia*, parasitoids, and palila. Specifically, it would allow us to determine whether these two ichneumonid species fill a natural role, or whether they are introductions with the potential to disrupt the equilibrium of trophic relationships.

The remaining Ichneumonidae were intentionally or accidentally introduced. Three species of Ichneumonidae were purposely introduced as biocontrol agents. *Eriborus sinicus* (Holmgren) was introduced in 1895 to control the rice-borer *Chilo suppressalis* (Walker; Crambidae; Beardsley 2000). *Ichneumon purpuripennis* Cresson was introduced in 1928 to control *Spodoptera exigua* (Huebner) and *S. mauritia* (Boisduval), both pests of sugar cane (Funasaki *et al*. 1988). *Spilichneumon superbus* (Provancher) was introduced prior to 1909 to control armyworms (Beardsley 2000). Other species may also have been intentional introductions in the early days of biocontrol, when accurate records were not always kept (Gruner 2004). Most species, however, were introduced accidentally. This emphasizes the need to prevent future accidental introductions, since many exotic species are easily able to establish in native ecosystems.

The Braconidae in the pan traps were dominated by the sub-family Aphidiinae, which are small braconids that parasitize aphids (Homoptera: Aphididae; Goulet and Huber 1993). Since all aphids in Hawaiʻi are non-native, these species may be beneficial in preventing aphids from damaging native plants. In the malaise traps, the most dominant braconid species was *Meteorus laphygmae*. This species was purposely introduced in 1942 to control a wide variety of Lepidoptera pest species (Funasaki *et al*. 1988). It has been reared from foliage-living caterpillars on Mauna Kea (see Chapter 20: Threats to Food Resources: Foliar Caterpillar Parasitism), and could therefore be negatively affecting caterpillar populations. *Aspilota konae* was the only endemic species of braconid collected (Nishida 2002), though its origin is also questioned, as Beardsley (1980) listed it as introduced. A second species, *Aspilota* sp. A, not present in the key to Hawaiian Braconidae (Beardsley 1961), may be an undescribed endemic species, or a new introduction.

Ants

The upper boundary of Argentine ants within the mitigation parcel (~2,100 m) we delineated is unlikely to be the upper limit of their potential range. Argentine ants have been found near 2,400 m elevation on the western slope of Mauna Kea (see Chapter 22: Threats to Food Resources: Ants) and at 2,850 m on Haleakalā (Krushelnycky *et al*. 2005). Additionally, there are no barriers or distinct ecotones that would prevent a further spread upslope or along contour into potential palila habitat. Therefore, the population may still be expanding. Because the Argentine ant is a generalist forager that with overwhelming numbers can subdue a wide range of arthropod prey, including caterpillars, they have great potential to affect the availability of arthropod prey for palila; therefore, future surveys are warranted to monitor their spread. Additionally, testing control measures with the aim of eliminating the relatively small population at the gorge crossing below Puʻu Mali Cabin could prove worthwhile in preventing the spread of ants into nearby Palila Critical Habitat.

Cardiocondyla kagutsuchi appears to be less of a threat than the Argentine ants, since it has less impact on native ecosystems (Krushelnycky and Reimer 1996), and is not present in high abundance. However, surveys on the western slope of Mauna Kea (U.S. Geological Survey unpublished data) have shown that *C. kagutsuchi* is not consistently attracted to baits, even when present in the vicinity of the bait station. Therefore, the absence of detected *C. kagutsuchi* over much of the surveyed area may indicate a low density, rather than an absence of this species. Continued monitoring, which should include sampling under rocks, is needed to determine whether the population of *C. kagutsuchi* is increasing, and further studies would help determine the ecology and potential impacts of this species.

Other Hymenoptera

Vespula pensylvanica and *Polistes* sp. prey upon other arthropods with potential consequences for the native arthropod community and food availability for the palila (see Chapter 21: Threats to Food Resources: Yellowjackets). Although we did collect *Vespula* and *Polistes*, the methods we used are not as effective as targeted, baited surveys for determining abundance, distribution, and seasonality of these wasps (Davis *et al.* 1969, MacDonald *et al*. 1973).

Native bees, such as endemic species of *Hylaeus*, may facilitate the reproduction of many native plants. They probably face considerable competition from introduced pollen gatherers, such as honeybees (*Apis mellifera*; Daly and Magnacca 2003), and nectar robbers, such as *Vespula pensylvanica* (Hanna *et al.* 2013). Additionally, Argentine ants have been found to decrease *Hylaeus* populations on Haleakalā, Maui, through depredation of their nests (Cole *et al*. 1992). Depending on interactions with honeybees and ants and the extent of forest restoration, we would expect *Hylaeus* bee populations to increase with greater access to native flowering plants (Hanna *et al.* 2013).

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19 THREATS TO FOOD RESOURCES: *CYDIA* CATERPILLAR PARASITISM

Peter T. Oboyski, Paul C. Banko

Introduction

Caterpillars of *Cydia* spp. (Lepidoptera: Tortricidae) feed inside māmane seeds and can be found within māmane pods throughout subalpine Mauna Kea (see Chapter 16: Food Availability: Māmane Phenology and *Cydia* Caterpillars). *Cydia* caterpillars are important in the diet of palila, especially nestlings (see Chapter 14: Diet), and their availability may affect palila productivity. Preliminary attempts to rear *Cydia* moths from māmane pods revealed that these caterpillars were parasitized by several species of parasitoid wasps. We initiated two captive-rearing studies to determine the distribution, species, and abundance of *Cydia* and their associated parasitoids within palila habitat. The first study (Brenner *et al.* 2002) focused on study grids located primarily on the western slope of Mauna Kea. The second study (Oboyski *et al.* 2004) explored parasitism patterns in dry, subalpine forests around Mauna Kea.

Methods

Cydia caterpillars were reared in the laboratory from māmane pods collected in the field during 1997 (Brenner *et al.* 2002) and 1998−2001 (Oboyski *et al.* 2004). Pods were inspected for *Cydia* by noting the presence of silk caps that were spun by caterpillars over their emergence holes. In the 1997 study, we collected pods from eight sites located on the northern, western, and southern slopes of Mauna Kea and two sites within Pōhakuloa Training Area (PTA; see Introduction, Figure I.1), representing an elevation gradient ranging from 1,700–2,800 m elevation. In the 1998–2001 study, we stratified sampling according to four slopes (N, S, E, W) and five bands of elevation (2,200, 2,350, 2,500, 2,650, 2,800 m). During the first study, we collected 10 pods from each study site each month from April 1996 to April 1997. During the second study, we collected 25 pods quarterly (February, May, August, November) from each elevation band and each slope of the mountain. Sample locations coincided with māmane phenology sites around Mauna Kea (see Chapter 16: Food Availability: Māmane Phenology and *Cydia* Caterpillars). No pods were collected at the lower elevations on the eastern slope of Mauna Kea due to the scarcity of māmane trees there (Figure 19.1).

We transported pods to Kīlauea Field Station (~1,200 m elevation) in Hawaiʽi Volcanoes National Park, where we reared moths and parasitoids at ambient temperature and humidity. Each pod was placed in a 240-ml plastic container in the laboratory and fitted with screen lids to allow air circulation and prevent molding. Containers were inspected daily for the emergence of moths and parasitic wasps. After three months, pods from which no insects emerged were dissected and the fate of each caterpillar was recorded (e.g., alive, dead, missing, never present). Live caterpillars were returned to their pods to finish development. We recorded the number and type of specimen that emerged and the date and location of pod collection.

We calculated parasitism rates as the proportion of wasps that emerged out of all emerging specimens. Linear regression was used to analyze the relationship between parasitism rates and elevation. Only samples from the southern, western, and northern slopes were used to examine the relationship between elevation and parasitism because we could not obtain pods at lower elevations on the eastern slope. Fisher's exact test (unadjusted values) was used to compare parasitism rates among the three slopes.

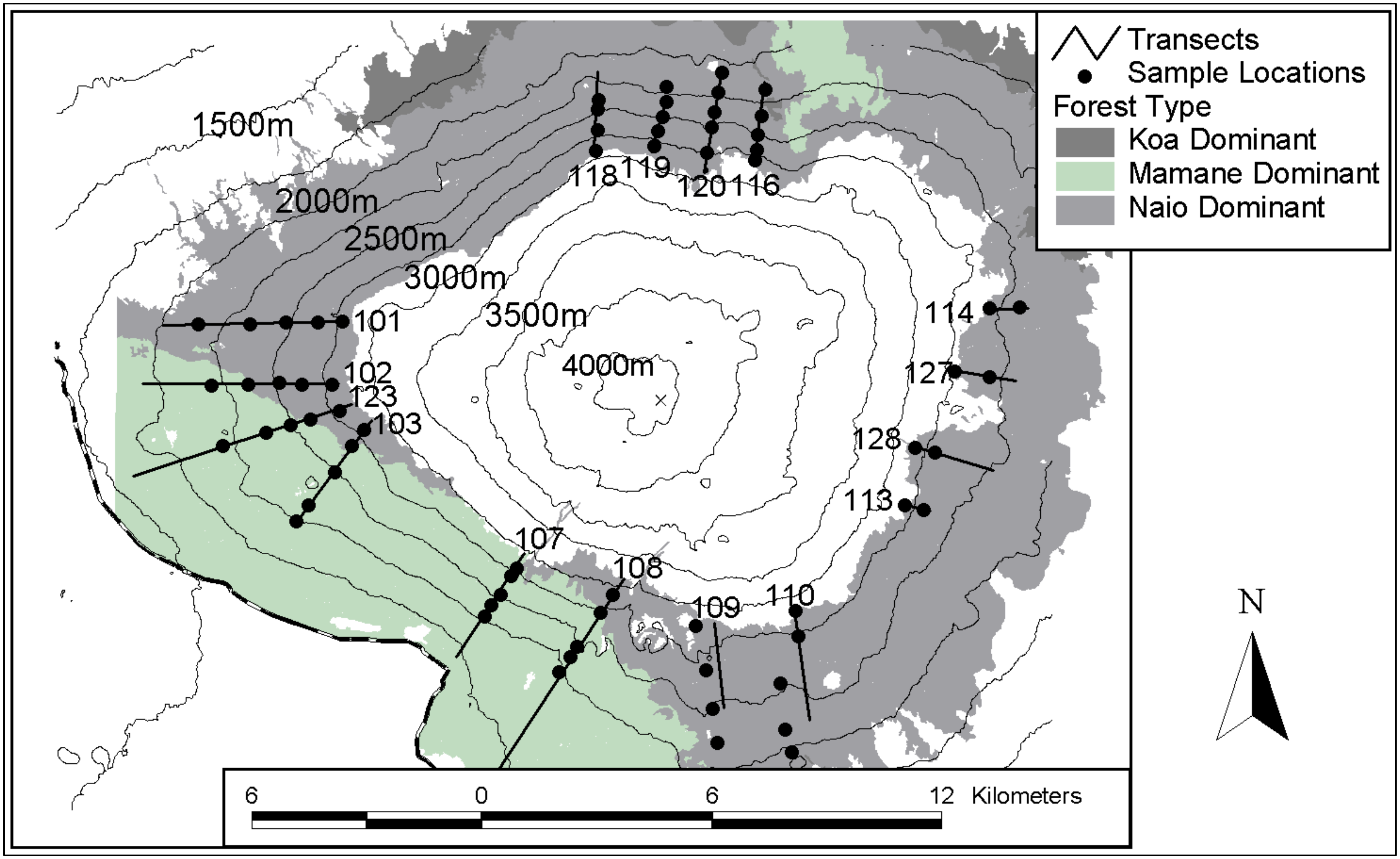

Figure 19.1. Sample locations for *Cydia* parasitism study along transects on Mauna Kea, Hawai'i, during 1998–2001.

Results

During the 1997 study, we reared 282 *Cydia* moths and 194 parasitic wasps of four species (Brenner *et al.* 2002). Parasitism of *Cydia* ranged from 21% at PL Mauka to 94% at PFlats and Kīpuka ʻAlalā. Parasitism decreased as elevation increased ($r^2 = 0.89$, $P < 0.01$; Figure 19.2). *Pristomerus hawaiiensis* Perkins (Ichneumonidae) accounted for 51% of the parasitism overall, and parasitism by this wasp decreased with elevation (Figure 19.3). *Euderus metallicus* (Ashmead; Eulophidae) parasitized *Cydia* at moderately low levels (~10%) across all elevations. *Calliephialtes grapholithae* (Cresson; Ichneumonidae) emerged most frequently from pods collected at lower elevations (≤47% at PFlats), while *Diadegma blackburni* (Cameron; Ichneumonidae) appeared most often from pods obtained at higher elevations (≤7% at PL Makai).

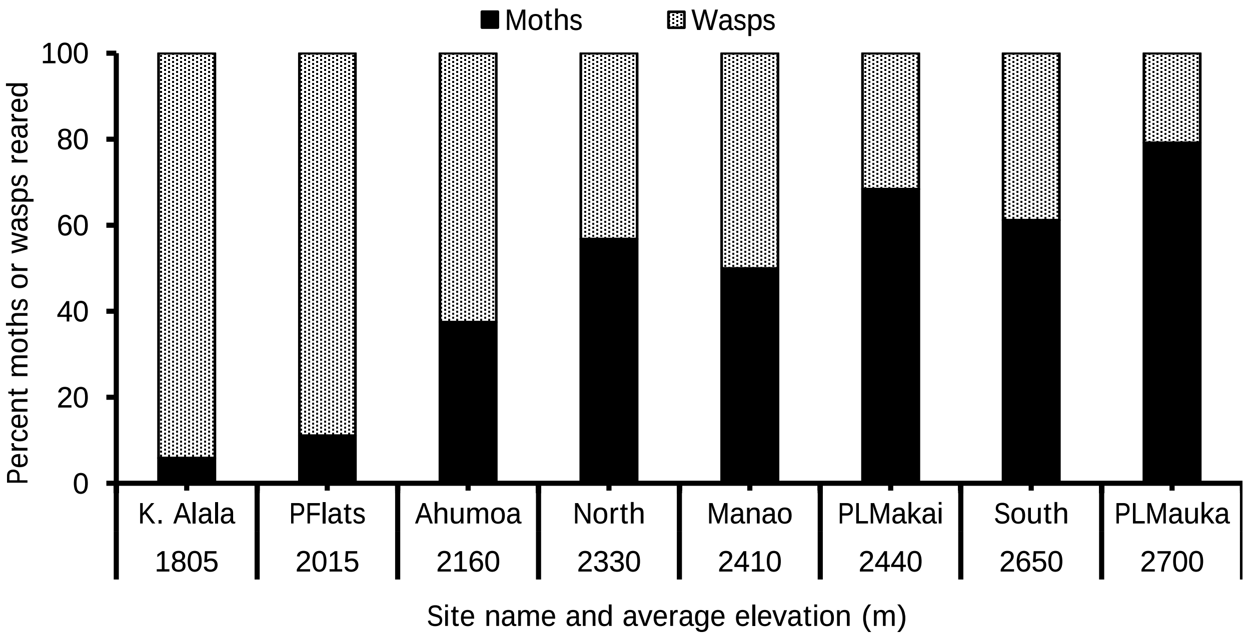

Figure 19.2. Percent of *Cydia* caterpillars from Mauna Kea, Hawaiʻi, that were reared to moths or parasitized in 1997 (Brenner *et al.* 2002).

During the 1998–2001 study (Oboyski *et al.* 2004), *Cydia* caterpillars were parasitized by the same four wasp species as in 1997 (Figure 19.4). Parasitism pooled across all slopes and all elevations was 38% (458 of 1,200 caterpillars). *Euderus metallicus* accounted for 20% of all specimens (both wasps and moths) reared and 51% of all wasps reared. Of all specimens reared, 7% were *Pristomerus hawaiiensis* (20% of all wasps), 8% were *Diadegma blackburni* (22% of all wasps), and 3% were *Calliephialtes grapholithae* (7% of all wasps). Parasitism by *E. metallicus* increased significantly with elevation (adjusted $r^2 = 0.81$, $P < 0.05$), ranging from 8% at 2,200 m to 26% at 2,650 m (Figure 19.5). Parasitism by *P. hawaiiensis* and *C. grapholithae* decreased significantly with elevation ($r^2 = 0.94$, $P < 0.05$; and $r^2 = 0.80$, $P < 0.05$, respectively) from 20% and 10% at 2,200 m to 2% and 0% at 2800 m, respectively. Parasitism by *D. blackburni* was not significantly related to elevation ($r^2 = 0.25$). Parasitism did not vary

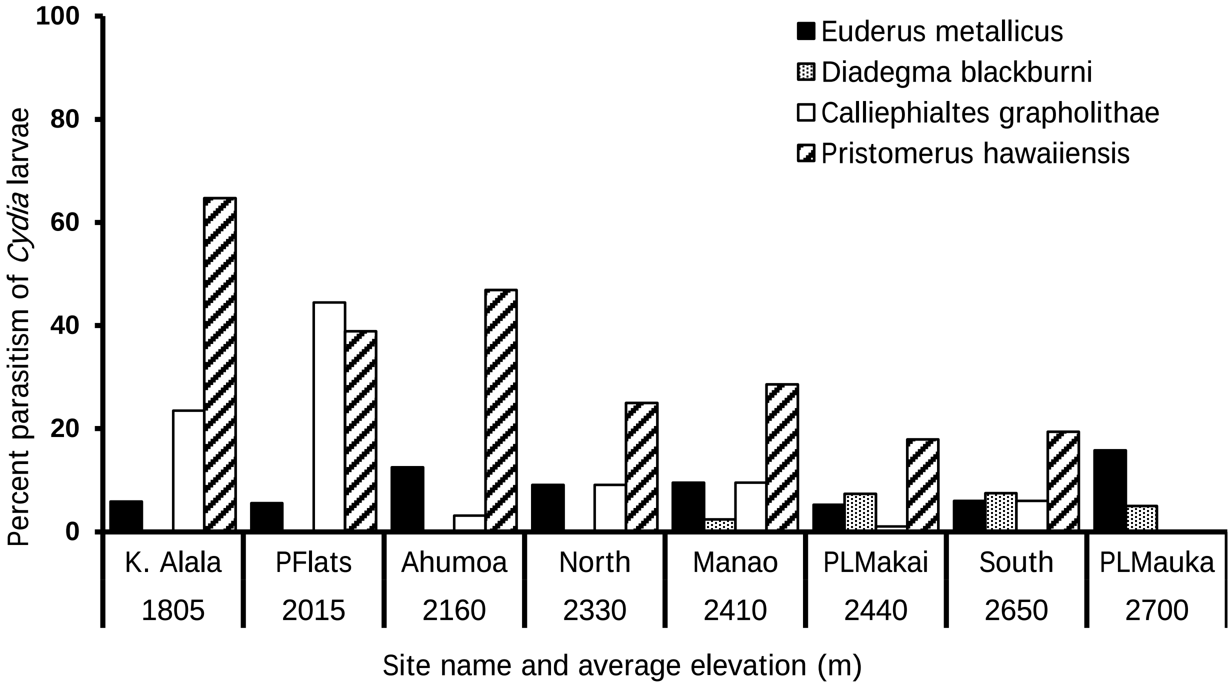

Figure 19.3. Percent of *Cydia* caterpillars parasitized by each of four wasp species at eight sites on Mauna Kea, Hawai'i, in 1997 (Brenner *et al.* 2002). Percent parasitism adds to less than 100%; the remainder of the caterpillars were successfully reared to adult moths.

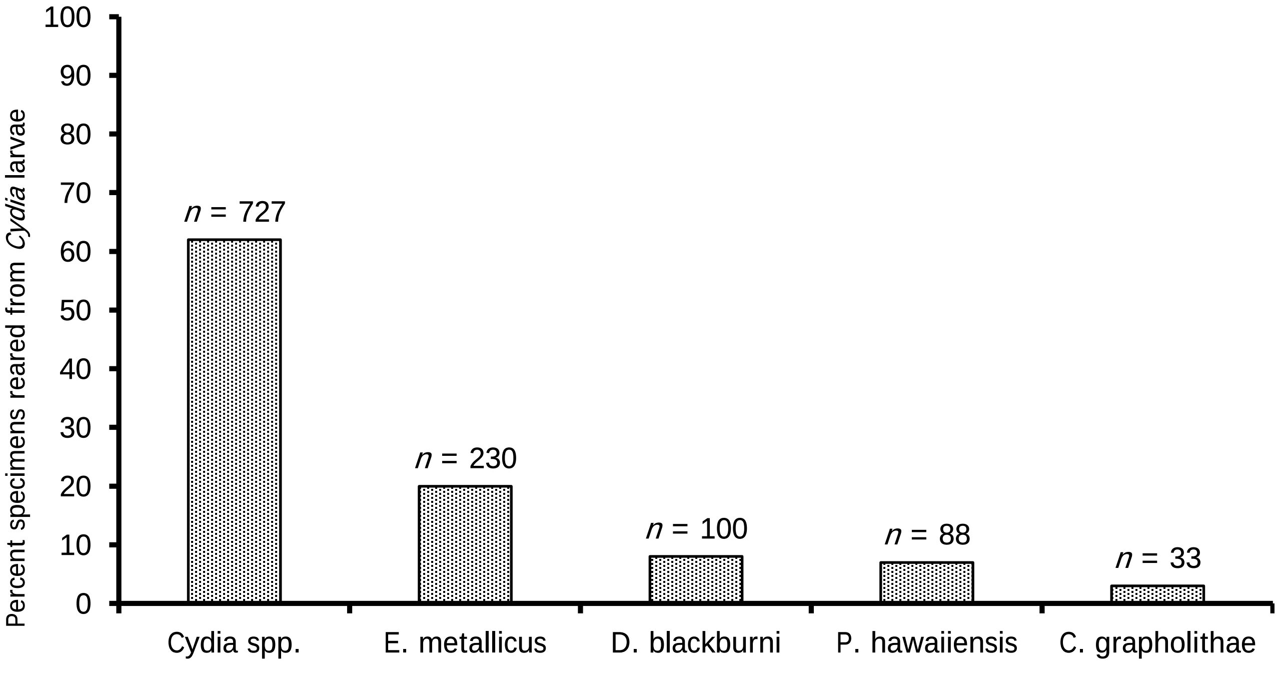

Figure 19.4. Percent of moths or wasps reared from *Cydia* caterpillars from Mauna Kea, Hawai'i, 1998–2001 (Oboyski *et al.* 2004).

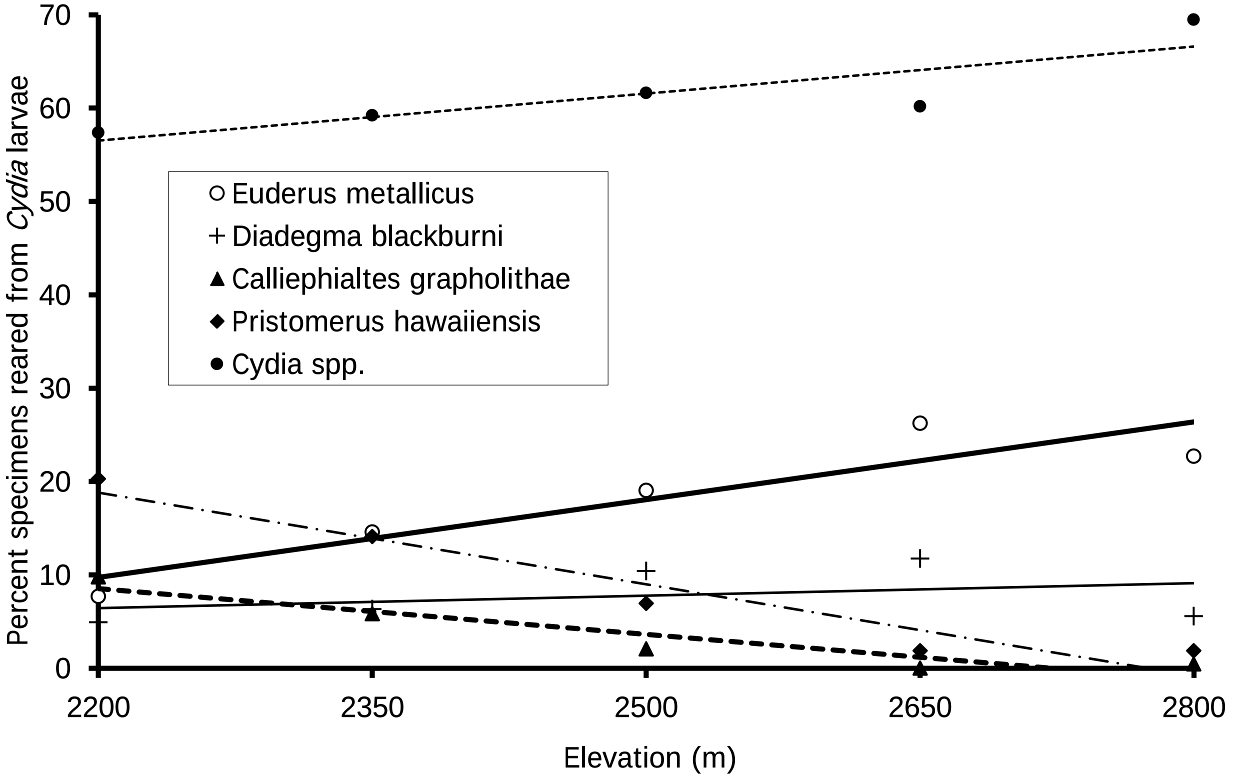

Figure 19.5. Percent parasitism of *Cydia* by elevation on Mauna Kea, Hawai'i, 1998–2001 (Oboyski *et al.* 2004).

significantly with slope for any of the four wasp species (Figure 19.6). There was no significant difference in overall parasitism (all wasp species) for either the southern, western, or northern slopes (Fisher's exact test, $P > 0.10$ for all pairwise comparisons). The eastern slope was not used for comparison due to a lack of sample size from lower elevations.

Discussion

Cydia spp. caterpillars that feed on māmane seeds on Mauna Kea were parasitized by four wasp species (Brenner *et al.* 2002, Oboyski *et al.* 2004). *Pristomerus hawaiiensis*, *Calliephialtes grapholithae*, *Diadegma blackburni*, and *Euderus metallicus* were each reared from *Cydia* caterpillars; the latter three being new host associations. Historically, *P. hawaiiensis*, *Trathala flavo-orbitalis* (Cameron; Ichneumonidae) and *Eupelmus pelodes* Perkins (Eupelmidae) were known to parasitize *Cydia* caterpillars in Hawai'i (Perkins 1913, Swezey 1954, Zimmerman 1978). We did not recover *T. flavo-orbitalis* or *E. pelodes* from *Cydia* caterpillars.

In both the 1997 and 1998–2001 studies, parasitism rates by different wasp species varied with elevation. Overall parasitism decreased with elevation in 1997, due mostly to the high incidence of two wasp species at lower elevations (*C. grapholithae* and *P. hawaiiensis*) and the inclusion of two low elevation sites in PTA. In the 1998–2001 study, overall parasitism did not vary significantly with elevation, although parasitism by particular wasp species was related to elevation.

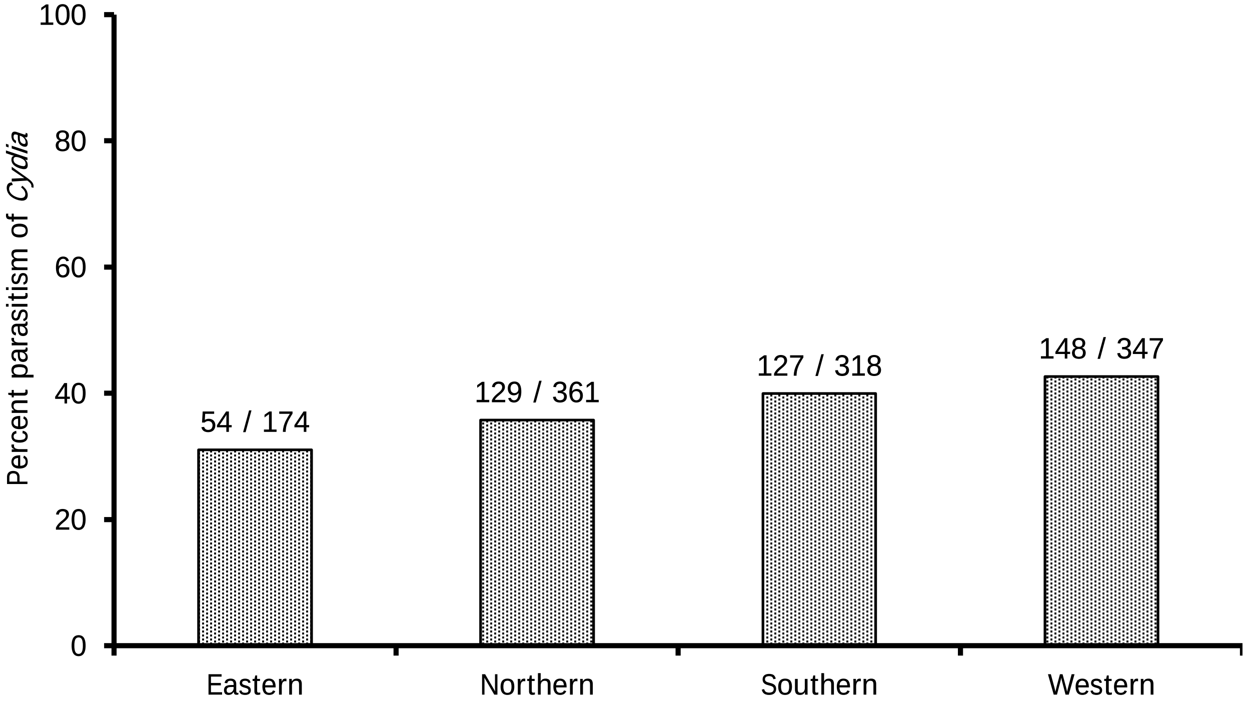

Figure 19.6. Percent parasitism of *Cydia* by four wasp species on four slopes of Mauna Kea, Hawai'i, 1998–2001 (Oboyski *et al.* 2004). Proportion of the total individuals parasitized are shown above the bars.

A major difference between the two studies was the increased rate of parasitism by *E. metallicus* in 1998–2001, particularly at higher elevations, and the decreased rate of parasitism by *P. hawaiiensis* during 1998–2001 (Oboyski *et al.* 2004). In 1997, *E. metallicus* was distributed more evenly across all elevations. Each wasp species is a generalist parasitoid that attacks caterpillars from many families in many habitats across a wide elevation range (Swezey 1954, Zimmerman 1978). We reared *P. hawaiiensis* from *Cydia* collected at 3,000 m on the western slope of Mauna Kea, however, *P. hawaiiensis* and *C. grapholithae*, two of the ichneumon species, were more prevalent at lower elevations (U.S. Geological Survey unpublished data). This limitation in elevation may result from competition with *E. metallicus*, which seems to be more prolific at higher elevations. Although *D. blackburni* emerged from *Cydia* less often than the other wasps in most areas, it was commonly reared from the native koa butterfly, *Udara blackburni* (Tuely; Lycaenidae) on Mauna Kea (U.S. Geological Survey unpublished data).

The ichneumon wasp, *C. grapholithae*, is thought to be alien to Hawai'i. *D. blackburni* and *P. hawaiiensis* are probably native to Hawai'i since *P. hawaiiensis* has never been reported outside Hawai'i and the one report of *D. blackburni* in Oregon is suspect (Fullaway and Krauss 1945; Nishida 2002; J. Beardsley, University of Hawai'i at Mānoa, personal communication). Although their status may be uncertain, *P. hawaiiensis* and *D. blackburni* were collected in Hawai'i in the late 1890s (Perkins 1913), while *C. grapholithae* was not discovered until the late 1940s (V. Jones, University of Hawai'i at Mānoa, personal communication). The eulophid wasp, *E. metallicus*, has been collected in Hawai'i and Guam and may be indigenous to several Pacific archipelagos (J. Beardsley, University of Hawai'i at Mānoa, personal communication). It parasitizes caterpillars of *Cydia* and species of many other families. These results suggest that parasitic wasps, many of which have been present on Mauna Kea for over 100 years, are partitioning the landscape and its resources.

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20 THREATS TO FOOD RESOURCES: FOLIAR CATERPILLAR PARASITISM

John W. Slotterback, Peter T. Oboyski, Paul C. Banko

Introduction

Foliar-feeding caterpillars are important food for developing chicks and adults of many Hawaiian forest bird species (Perkins 1913). While feeding on foliage, these caterpillars are vulnerable to parasitism by many species of wasps and flies, some native and others introduced. Many species of parasitoids have been introduced to Hawaiʽi since the early 1900s to control agricultural pests (Funasaki *et al*. 1988). Several of these are generalists with respect to host preferences and are capable of attacking a wide variety of caterpillar species. The impact of these alien parasitoids on native species in natural habitats has not been evaluated until recently (Henneman and Memmott 2001, Brenner *et al.* 2002, Oboyski *et al.* 2004), but reduced caterpillar abundance may have contributed to the historical decline of native Hawaiian forest birds (Banko and Banko 2009).

Two endemic species, *Scotorythra artemidora* Zimmerman (Lepidoptera: Geometridae) and *Peridroma albiorbis* (Lepidoptera: Noctuidae), composed 99% of the caterpillars feeding on māmane (*Sophora chrysophylla*) foliage on Mauna Kea (see Chapter 17: Food Availability: Foliar Caterpillars). Preliminary rearing trials revealed that non-native flies and wasps preyed on both caterpillar species, suggesting that these parasitoids may reduce the availability of insect prey for native birds. We reared caterpillars collected from the northern and western slopes of Mauna Kea to determine the incidence of parasitism of foliar-feeding caterpillars.

Methods

Caterpillars were collected along an elevation gradient on the northern and western slopes of Mauna Kea (Figure 20.1) from January 1998 to October 2000. Caterpillars were reared at ambient temperature and humidity at Kīlauea Field Station (~1,200 m elevation) in Hawaiʽi Volcanoes National Park. Each caterpillar was placed in an individual 240-ml cup and given fresh foliage from host plants at least twice per week. Rearing cups were checked daily for the emergence of an adult moth or parasitoid wasp or fly. Parasitism rates were calculated as the proportion of all specimens that emerged as wasps. Linear regression was used to analyze the relationship between parasitism rates and elevation.

Results

Five parasitoid species emerged from three caterpillar species collected from three host plants (Table 20.1). *Scotorythra artemidora* collected from māmane was the most common caterpillar encountered in our sampling. *Peridroma albiorbis* caterpillars were collected from māmane and ʽāheahea (*Chenopodium oahuensis*), whereas the endemic koa butterfly, *Udara blackburni* (Tuely; Lepidoptera: Lycaenidae), was collected from ʻaʽaliʽi (*Dodonaea viscosa*). Parasitism rates varied among the five parasitoids (Table 20.1), which included two ichneumon wasps, *Hyposoter exiguae* (Viereck), *Diadegma blackburni* (Cameron; Hymenoptera: Ichneumonidae); two braconid wasps, *Meteorus laphygmae* Viereck and *Cotesia* sp. (Hymenoptera: Braconidae); and a fly, *Chaetogaedia monticola* (Bigot; Diptera: Tachinidae).

Parasitism of *Scotorythra artemidora* caterpillars declined with increasing elevation ($r^2 = 0.90$; $P = 0.013$), ranging from 43% at 2,200 m elevation to 22% at 2,800 m when samples from the northern and western slopes were pooled (Figure 20.2). A total of 44 of 171 (26%) *Scotorythra* caterpillars were parasitized. Parasitoids included *H. exiguae*, *D. blackburni*, *M. laphygmae*, and

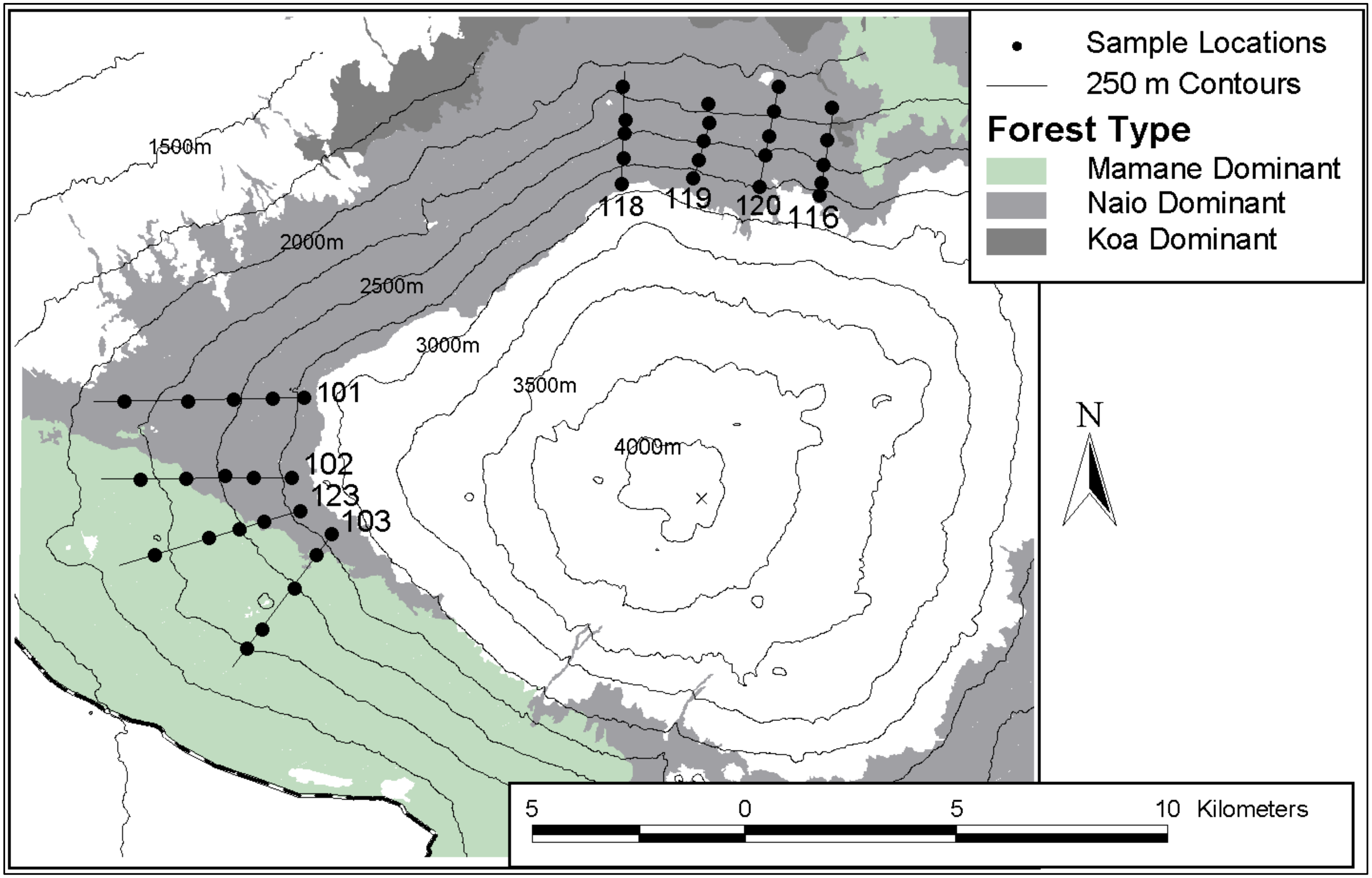

Figure 20.1. Foliar caterpillar sample sites along transects on western and northern slopes of Mauna Kea, Hawai'i, during 1998–2000.

C. monticola (Table 20.1). Parasitism rates were not compared between the northern and western slopes and among caterpillar species due to small and unequal sample sizes. *Peridroma albiorbis* was also parasitized by *H. exiguae*, *D. blackburni*, and *C. monticola* (Table 20.1). *C. monticola* parasitized *Scotorythra* and *Peridroma* caterpillars when they were on māmane but did not parasitize *Peridroma* caterpillars on ʽāheahea. The only specimens of *Cotesia* wasps emerged from a *Peridroma* caterpillar collected on ʽāheahea. *Udara blackburni*, found only on ʻaʽaliʽi, was parasitized only by *Diadegma blackburni*. The sample of *Peridroma* and *Udara* specimens was insufficient for analyzing elevation trends (Figure 20.2).

Table 20.1. Parasitism of foliar-feeding caterpillars on Mauna Kea, Hawaiʽi, 1998–2000. Shown are the number of moths (no parasitoids) and parasitoids that emerged from three caterpillar species (*Scotorythra artemidora*, *Peridroma albiorbis*, *Udara blackburni*) collected from three host plants (*Sophora chrysophylla*, *Chenopodium oahuensis*, *Dodonaea viscosa*).

Parasitoid	Genus: Host:	*Scotorythra* *Sophora*	*Peridroma* *Sophora*	*Peridroma* *Chenopodium*	*Udara* *Dodonaea*
Hyposoter exiguae		33	6	4	0
Diadegma blackburni		5	1	0	6
Meteorus laphygmae		3	0	0	0
Cotesia sp.		0	0	1	0
Chaetogaedia monticola		3	2	0	0
	Total parasitoids	44 (26%)	9 (26%)	5 (17%)	6 (17%)
	Moths	127 (74%)	26 (74%)	25 (83%)	30 (83%)
	Grand total	171	35	30	36

Discussion

Parasitoids are well established in the dry, subalpine environment of Mauna Kea. The dominant parasitoid, *Hyposoter exiguae*, was alien. Parasitism rates reached 47% in *Peridroma albiorbis* at 2,650 m elevation, indicating their potential for limiting the availability of this common caterpillar to foraging birds. Palila may have fed more frequently on foliar caterpillars in the past (Perkins 1913), but more recently they were not found commonly in the diet (see Chapter 14: Diet). This suggests that parasitoids could be reducing the recruitment of larvae into the moth population to the extent that palila are not encountering them frequently, even though birds may be ingesting parasitized caterpillars.

Five parasitoid species were reared from caterpillars on Mauna Kea. *Hyposoter exiguae* is an alien wasp that preys on many species of exposed caterpillars (i.e., those not hidden inside of fruits, seeds, or foliage bound together with webbing; Swezey 1954, Zimmerman 1958). *Diadegma blackburni*, likely a native parasitoid (Oboyski 2004, but see Nishida 2002), tends to attack caterpillars that bore into seeds or twigs, or that tie leaves together (Swezey 1954, Zimmerman 1978). Even so, we reared *D. blackburni* from caterpillars that feed on exposed leaves as well as *Cydia* caterpillars within māmane pods (Brenner *et al.* 2002, Oboyski 2004, see Chapter 19: Threats to Food Resources: *Cydia* Caterpillar Parasitism).

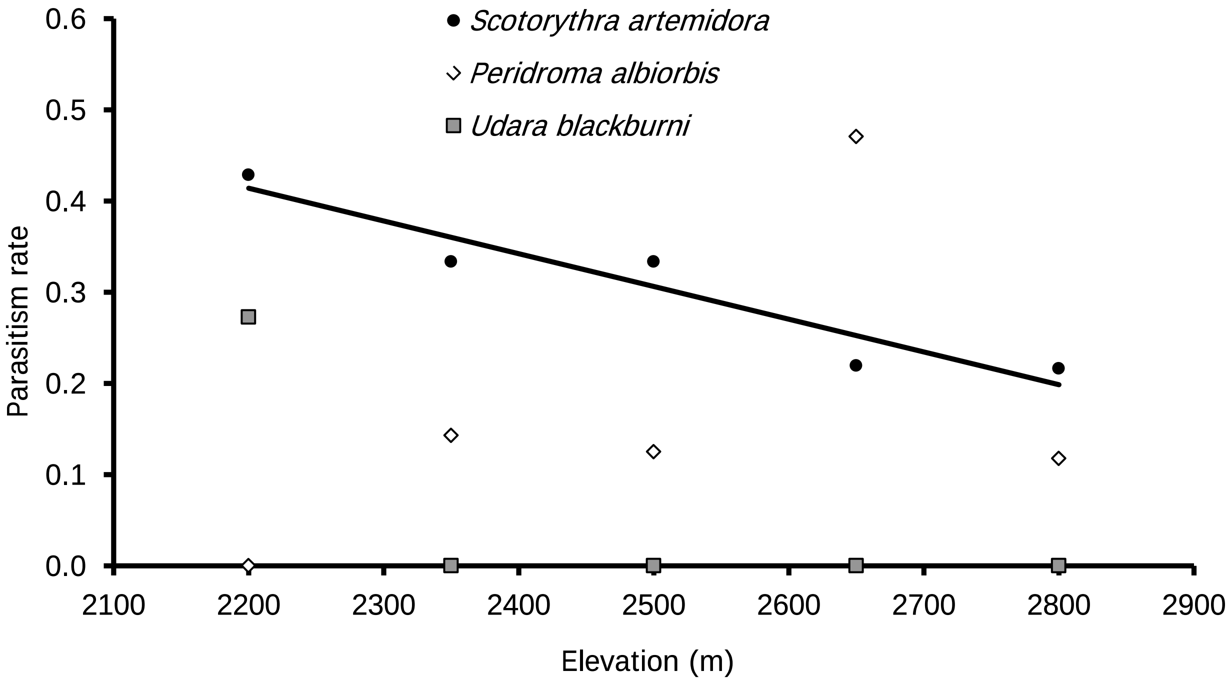

Figure 20.2. Percent parasitism by elevation of three foliar caterpillar species from the western and northern slopes of Mauna Kea, Hawai'i, 1998–2000. The trendline ($r^2 = 0.91$) is shown for *S. artemidora*, but for other species $r^2 \leq 0.5$. Data were pooled for specimens collected from the northern and western slopes.

The wasp, *Metorus laphygmae*, and the fly, *Chaetogaedia monticola*, were both purposefully introduced to Hawai'i to control agricultural pests (Funasaki *et al.* 1988). Although only three *Meteorus* wasps were reared from *Scotorythra artemidora* in this study, *M. laphygmae* was the most common wasp reared from *Scotorythra* n.sp.15 in Pōhakuloa Training Area training areas 1 and 2 (Oboyski *et al.* 2002). *Chaetogaedia* is a large fly that presumably requires larger hosts, such as late instar geometrid and noctuid caterpillars. After the fly larva has consumed most of its host's inner tissues, the caterpillar forms its pupal case from which the adult fly emerges. It is apparent that both of these parasitoid species have become established in the māmane forest of Mauna Kea and have adapted to attacking native hosts with potential consequences for food webs and bird diets.

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21 THREATS TO FOOD RESOURCES: YELLOWJACKETS

Kevin W. Brinck, Peter T. Oboyski, John W. Slotterback, Chris Farmer, David M. Pollock, Paul C. Banko

Introduction

Insect foods of palila (*Loxioides bailleui*) are vulnerable to predators in addition to parasites (see Chapter 19: Threats to Food Resources: *Cydia* Caterpillar Parasitism, and Chapter 20: Threats to Food Resources: Foliar Caterpillar Parasitism). One such threat is the invasive Western yellowjacket (hereafter "yellowjacket"), *Vespula pensylvanica* (Saussure; Hymenoptera: Vespidae), a generalist predator and scavenger. Since its arrival on Kauaʽi from the northwestern United States in 1919, yellowjackets have become established on all the major islands, including Hawaiʽi Island where it was initially discovered in 1978 (Nakahara and Lai 1981).

Previous studies of yellowjackets in the Hawaiian Islands have occurred on Haleakalā, Maui (Gambino *et al.* 1987, Gambino and Loope 1992), and Mauna Loa, Hawaiʽi Island (Gambino 1991, Spurr and Foote 2000), which with Mauna Kea are the only volcanoes in the archipelago higher than 3,000 m. As a temperate species, the yellowjacket is most common in the Hawaiian Islands above 800 m elevation, reaching its peak abundance at 2,600 m on Haleakalā (Gambino *et al.* 1990, Gruner and Foote 2000). This distribution is presumed to result from the interaction of rainfall and temperature and the species' physiological limits, but experimental studies have not yet been conducted (Gruner and Foote 2000).

Yellowjacket abundance typically follows a seasonal pattern with colony formation being an annual event. Where colonies overwinter, nests that grow for at least two seasons can achieve sizes up to 191,000 cells in California (Visscher and Vetter 2003) and 600,000 cells on Mauna Loa (Gambino and Loope 1992). Overwintering colonies may consist of 20 times the number of cells that annual colonies have with a concomitant higher foraging rate and negative impact on the local ecosystem (Gambino *et al.* 1990).

The establishment of yellowjackets in Hawaiʽi is feared to have far-reaching consequences because of its proclivity to prey on native arthropods, including caterpillars and spiders (Howarth 1985, Gambino *et al.* 1987, Gambino 1992) and compete for nectar and other floral resources (Hanna *et al.* 2013). Given the propensity of yellowjackets to prey on native insects, and a social structure that produces potentially large populations of foragers, the availability of insect foods of palila and other native birds may be reduced. Yellowjackets are most abundant at middle elevations (600–1,500 m) and upper elevations (2,500–2,700 m) on Maui (Gambino *et al.* 1990). On Hawaiʽi Island, yellowjackets have been studied within Hawaiʽi Volcanoes National Park on Mauna Loa (Gambino *et al.* 1987, Gambino and Loope 1992, Wilson *et al*. 2009, Hanna *et al*. 2013) but little is known about the distribution or natural history of yellowjacket populations on Mauna Kea. In this study we examined the occurrence of yellowjackets in dry, subalpine habitats between 2,200 and 2,800 m elevations on Mauna Kea to evaluate their potential threat to arthropods eaten by palila.

Methods

Survey Area

The study was conducted in subalpine habitat within Mauna Kea Forest Reserve and Kaʽohe Game Management Area (19°44′–19°55′N and 155°22′–155°37′W) in the state of Hawaiʽi.

Rainfall, wind, and associated plant communities in our study area were influenced by elevation and aspect of the slope (see Juvik and Nullet [1993] and Juvik *et al.* [1993] for climate details). Vegetation composition and structure varied around Mauna Kea, but the endemic māmane (*Sophora chrysophylla* [Salisb.] Seem.; Fabaceae) was the dominant or co-dominant tree species and three common endemic shrub species were widely distributed (U.S. Geological Survey unpublished data).

Naio (*Myoporum sandwicense* [A. Gray]; Myoporaceae), also endemic, was co-dominant with māmane over the entire southern slope, but naio trees were rare above 2,200 m elevation on the western slope and across the northern and eastern slopes. Pūkiawe shrubs (*Leptecophylla tameiameiae* [Cham. & Schlecht.] F. Muell.; Epacridaceae) were distributed around Mauna Kea; however, while they were abundant on the northern slope and very common on the eastern slope, they were relatively uncommon on the western and southern slopes. The next most widely distributed shrub species was ʽaʽaliʽi (*Dodonaea viscosa* [L.] Jacq.; Sapindaceae), which was common on the western and southern slopes, uncommon on the northern slope, and rare or absent on the eastern slope. ʽĀheahea (*Chenopodium oahuense* [Meyen] Aellen; Chenopodiaceae) was abundant on the western and southern slopes, but rare or absent elsewhere. Overall, the forest was more continuous and distributed over a larger area on the western and southern slopes. The forest on the northern slope was more open with several large areas of black volcanic sand. Forest on the eastern slope was highly fragmented and was narrowly distributed in elevation, being truncated below by pasturelands, where we did not set traps for yellowjackets.

Ground cover on all slopes consisted mainly of alien weeds and grasses, including *Dactylis glomerata* (L.), *Holcus lanatus* (L.), *Anthoxanthum odoratum* (L.), and *Poa pratensis* (L.), but endemic grasses tended to be more common in the higher elevations and on the northern slope. The soils were a mosaic of highly weathered ʽaʽā lava from eruptions occurring mainly between 4,000 and 14,000 years ago, but with some exposed patches ranging from 65,000 to 250,000 years ago (Wolfe and Morris 1996).

Data Collection and Analysis

We monitored yellowjacket activity monthly using Seabright™ brand traps baited with heptyl buterate, a known attractant for *Vespula pensylvanica* (Davis *et al.* 1969, MacDonald *et al.* 1973, Chang 1988), from June 1998 through November 2002. To prepare baits, the top 1 cm of a cotton swab was inserted into a 1.5 ml eppendorph tube filled with 75% heptyl buterate. Fresh baits were placed in the traps monthly when the traps were checked. The number of trapped yellowjackets was counted, dead arthropods were removed, and fresh bait was distributed to all the traps within a four-day period each month. A total of 68 traps were set in forested areas and adjacent pastures on the northern, southern, and western slopes of Mauna Kea at 2,200, 2,350, 2,500, 2,650, and 2,800 m elevations along transects (Figure 21.1). Because trees were scarce at lower elevations, we could only sample at 2,500, 2,650, and 2,800 m on the eastern slope (n = 8 traps), but the other slopes were sampled with 20 traps each. Traps were hung from a tree branch 1–2 m above ground at each sampling station. Traps were installed from May–August 1998 and were monitored until November 2002.

We searched for yellowjacket nests around traps that caught unusually large numbers of yellowjackets and around game bird watering stations where yellowjackets concentrated, but no systematic nest search attempts were made. Additionally, field crews working on other studies

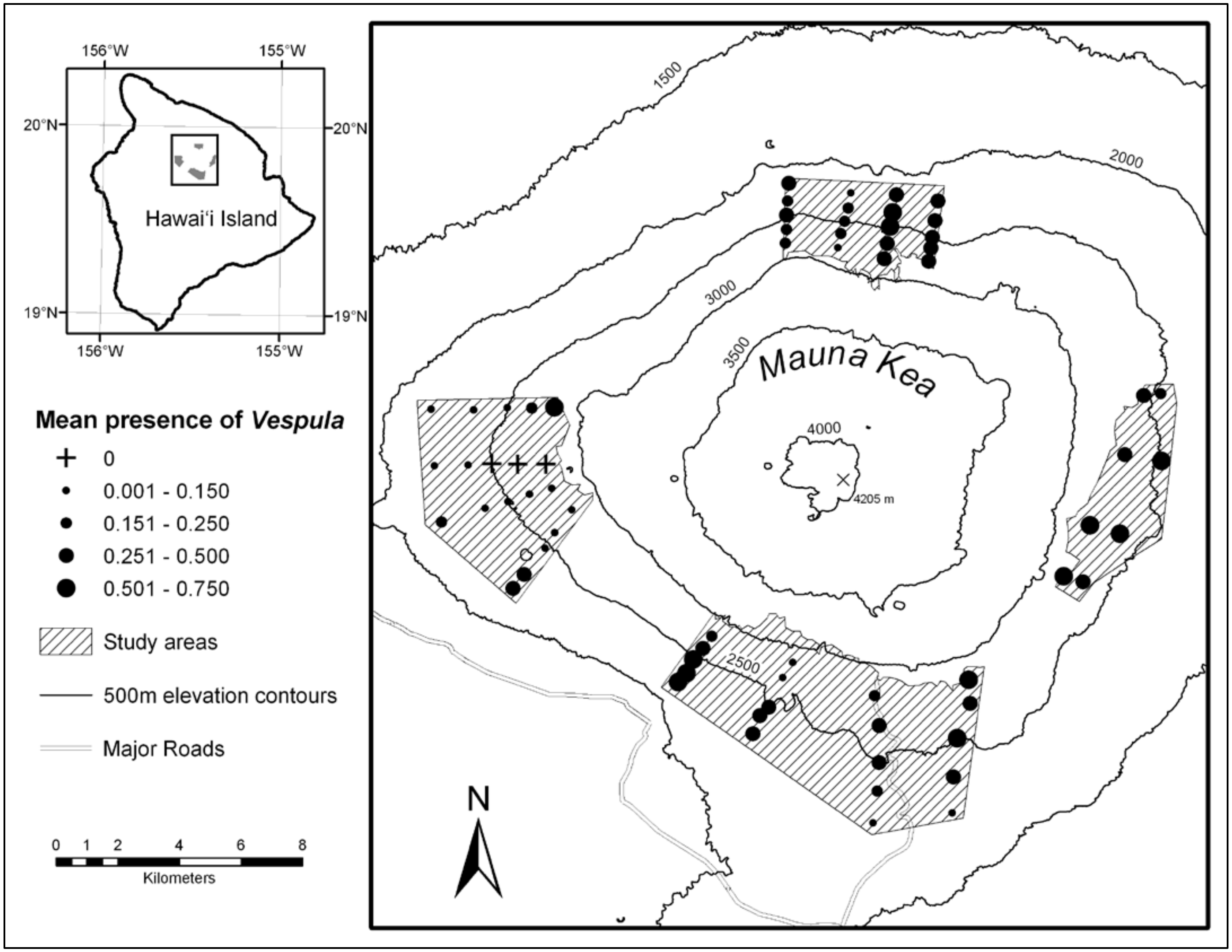

Figure 21.1. Sample locations and mean monthly capture rates of *Vespula pensylvanica* on Mauna Kea, Hawai'i, 1998–2002.

throughout the summer (primarily on the western slope) were instructed to report any findings of nests.

Trapping results from the eastern slope were analyzed separately from the other three slopes because we sampled only at the higher elevations. The qualitative pattern of yellowjacket captures was examined to make inferences regarding population expansion on Mauna Kea. Because there were many instances when traps were found empty, the formal data analysis used the presence or absence of yellowjackets in a trap in a given month in logistic regression models (S-Plus®, version 7.0) to identify the major factors affecting the distribution of yellowjackets on Mauna Kea. We included factors in the model if their probability of having a significant contribution was greater than 0.90. The presence or absence of yellowjackets in a trap each month was used as the response variable. The year, season, month, mountain slope (north, south, east, or west), and elevation were tested as categorical predictors. Elevation was also tested as both linear and quadratic continuous predictors.

Results

Yellowjackets were detected on all four slopes of Mauna Kea and in every month and year of the five-year study (Figure 21.1). The mean monthly abundance of yellowjackets per trap per slope ranged from 0 to 197. Yellowjackets were not found in 2,354 (72%) of the total 3,288 trap inspections carried out over the course of the study. The maximum number of individuals captured in a single trap was 695, and the mean over all slopes and years was 4.32 yellowjackets/trap. During the first year of our study, yellowjackets were most abundant on the northern slope (Figure 21.2A). In 1999, yellowjacket numbers in traps increased nearly 20-fold over all slopes, with the eastern slope having the largest number of yellowjackets and proportion of occupied traps (Figure 21.2A, B). The total annual abundance of yellowjackets never exceeded 51% of the 1999 peak in the remaining three years of our study.

On the northern, southern, and eastern slopes, yellowjackets were trapped at every station at some time during the study. On the western slope, however, yellowjackets were never caught in 3 of 20 traps along one transect (Figure 21.1). Overall, a smaller percentage of traps caught yellowjackets on the western slope than any other slopes (12% west vs. 32% north, 35% south, and 46% east).

The fraction of traps that caught yellowjackets in the first and last years of sampling was similar, increasing slightly from 27% in 1998 to 30% in 2002. However, patterns of yellowjacket occurrence over time varied by slope (Figure 21.2A, B). On the eastern slope, the incidence of yellowjackets was very high during the first two years with levels moderately lower in the remaining three years. On the northern slope, the incidence of yellowjackets fluctuated between moderately high and low levels throughout the study period. Yellowjacket occurrence at traps on the western and southern slopes was initially less than 25% of the incidence recorded on the eastern and northern slopes. Nevertheless, yellowjacket occurrence had doubled on the western slope by the end of the study, whereas their incidence on the southern slope abruptly increased 10-fold and remained at about these levels for the remainder of the study. The mean annual incidence of yellowjackets at traps was 28% across all years and slopes. Following a peak of 59% on the eastern slope in 1999, the mean annual incidence of yellowjackets converged to about 34% on the eastern, northern, and southern slopes by 2002, while yellowjacket occurrence at traps on the western slope doubled from 10% to 20% (Figure 21.3).

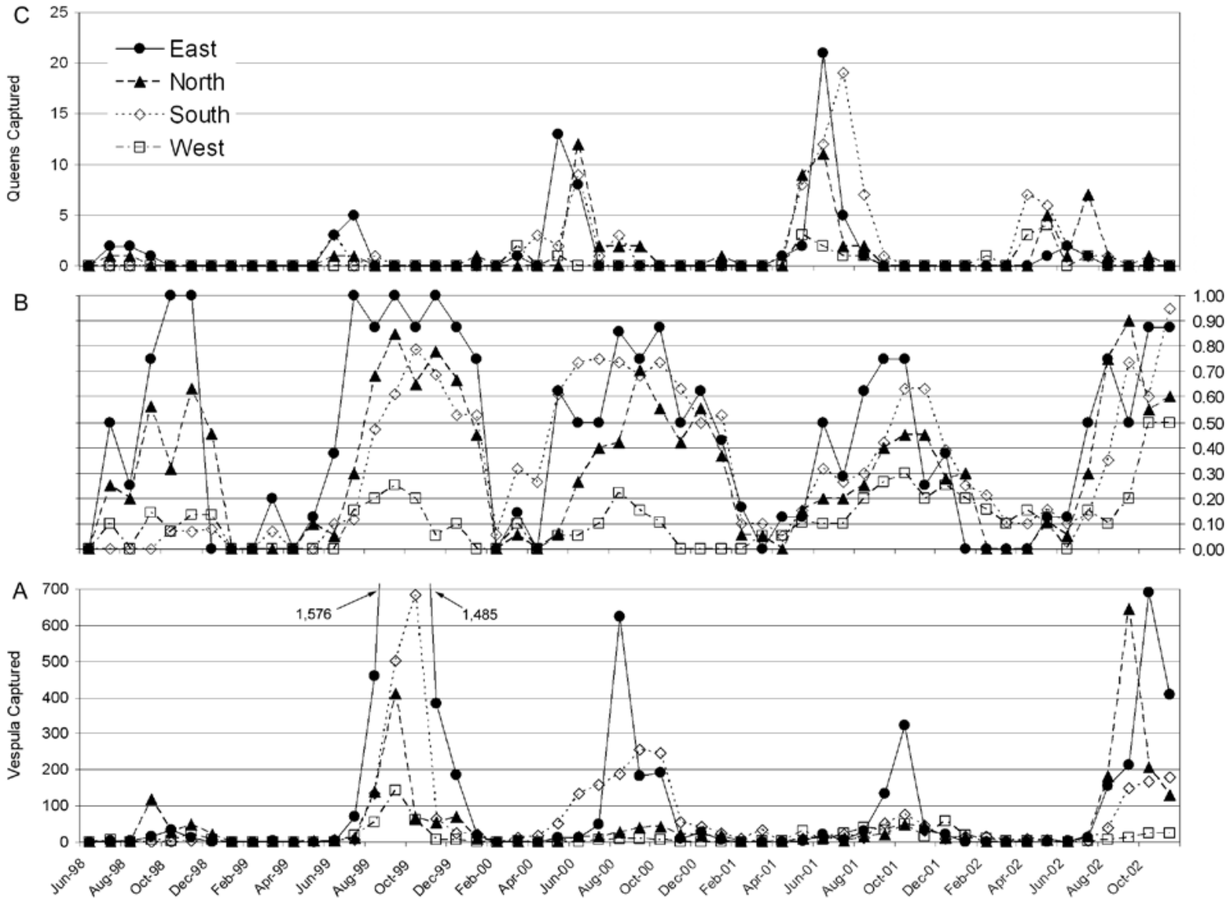

Figure 21.2. A) Total number of yellowjackets, B) proportion of traps containing yellowjackets, and C) total number of queens captured through each year on Mauna Kea, Hawai'i, during 1998–2002.

Yellowjacket queens were caught around Mauna Kea, and monthly captures in individual traps ranged from 0–15. The total annual catch of queens ranged from 7 (1998) to 110 (2001). Queen capture rates followed a roughly similar pattern on the southern, eastern, and northern slopes, and we captured the greatest numbers on the eastern and southern slopes in 2001 (Figure 21.2C). The abundance of queens tended to be highest in June, but they were caught in every month except November and December.

The regression model for the northern, southern, and western slopes identified year, month, slope, and elevation category as significant factors in determining yellowjacket presence (Table 21.1). Also significant were two-way interactions between slope and year, month and elevation, as well as the interactions between year and month and year and elevation. The model for the eastern slope selected year, month, and elevation as significant factors, and it identified the interaction between year and month as significant (Table 21.2). Seasonal variation, as indicated by month, had the strongest predictive influence on the incidence of yellowjackets in both models (Tables 21.1 and 21.2). Yellowjacket occurrence in traps peaked during September–November then fell to a minimum during February–April, following an approximate sine curve throughout the year (Figure 21.4). Year was also a significant effect in both models (Tables

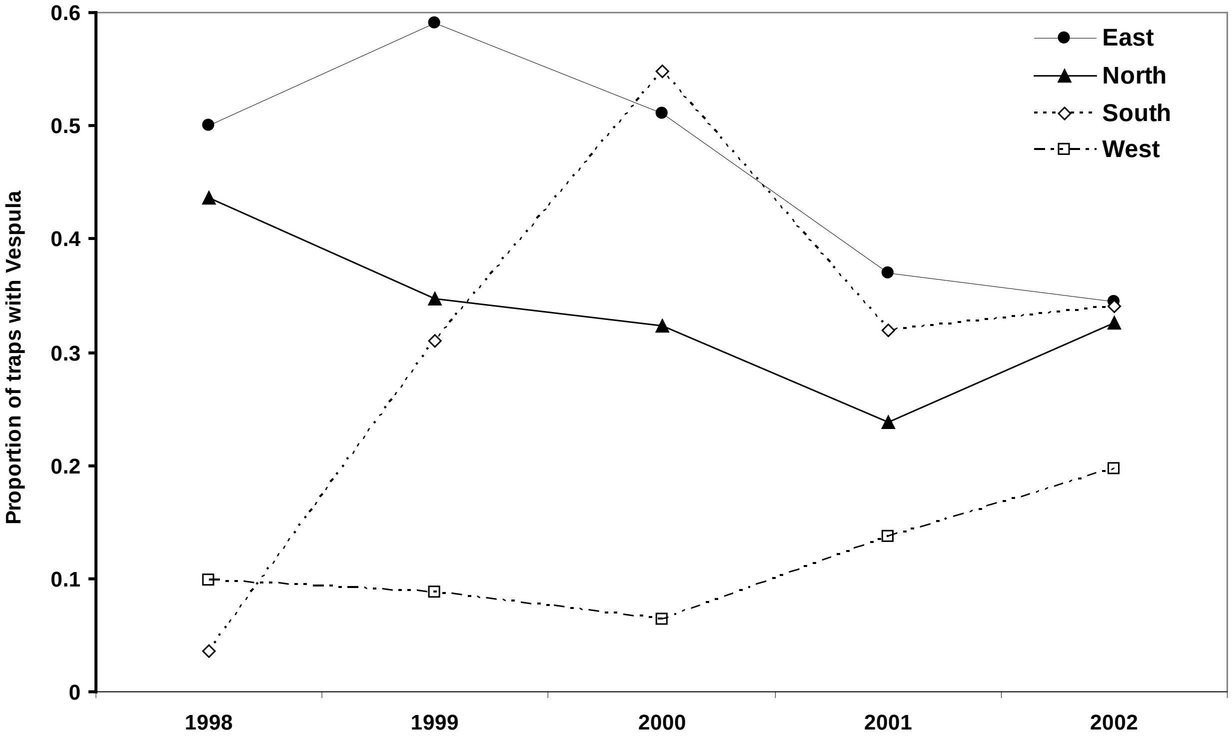

Figure 21.3. The annual mean proportion of traps within each slope that caught one or more yellowjackets (*Vespula*) on Mauna Kea, Hawai'i, during 1998–2002.

Table 21.5. Significant factors in yellowjacket incidence on the northern, western, and southern slopes of Mauna Kea, Hawai'i during 1998–2002. Residual degrees of freedom = 2,792.

	df	Deviance	F	*P*
Year	4	80	22.2	< 0.001
Month	11	394	39.7	< 0.001
Slope	2	199	110.0	< 0.001
Elevation	4	20	5.5	< 0.001
Slope:year	8	109	15.1	< 0.001
Slope:month	22	55	2.8	< 0.001
Slope:elevation	8	41	5.6	< 0.001
Year:month	38	125	3.7	< 0.001
Year:elevation	16	47	3.2	< 0.001

Table 21.2. Significant factors in yellowjacket incidence on the eastern slope of Mauna Kea, Hawai'i during 1998–2002. Residual degrees of freedom = 326.

	df	Deviance	F	*P*
Year	4	20.9	6.0	< 0.001
Month	11	140.5	14.6	< 0.001
Elevation	2	22.5	12.8	< 0.001
Year:month	38	82.8	2.5	< 0.001

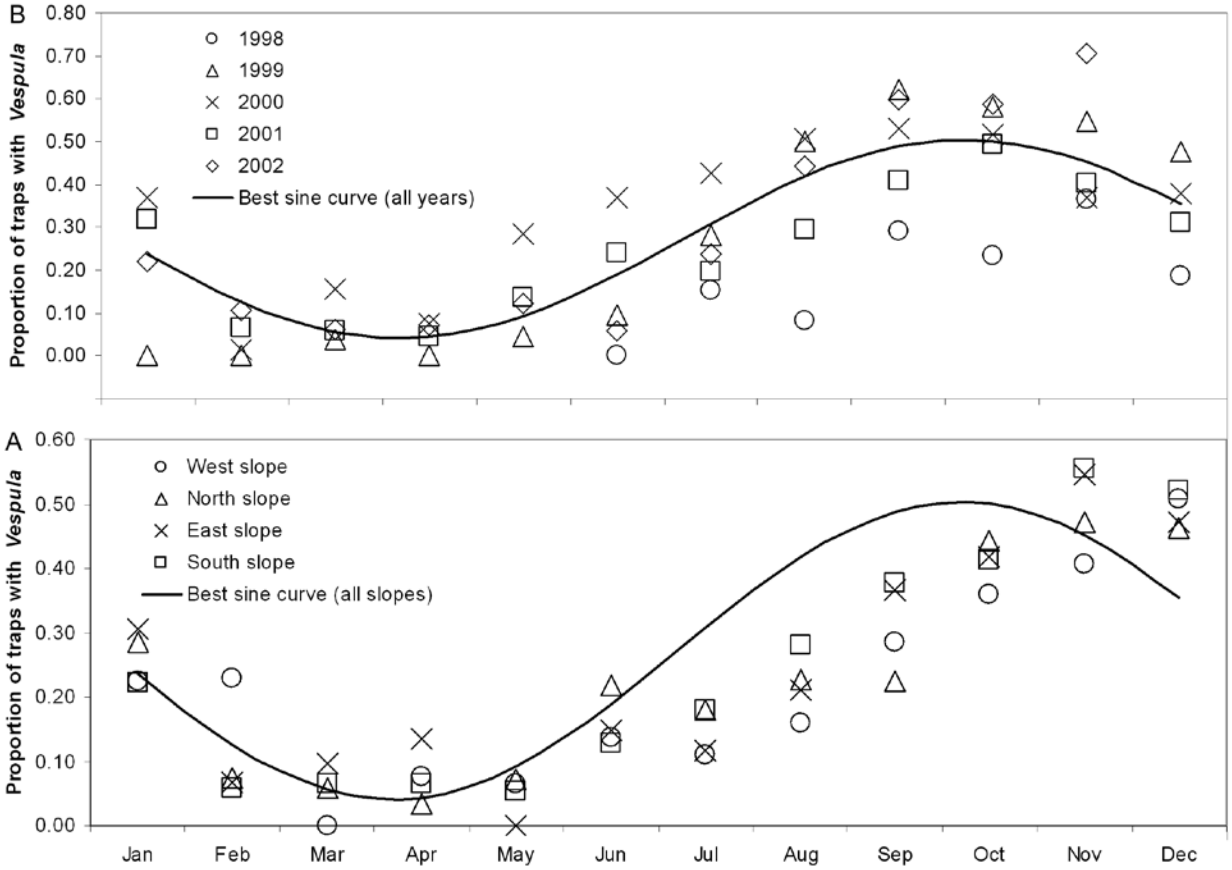

Figure 21.4. Mean proportion of traps that caught one or more yellowjackets, A) by slope and B) by year for all months. The fraction of traps by month fit an approximate sine curve for all slopes, though the relative amplitude varied between slopes.

21.1 and 21.2, Figure 21.3); however, after accounting for monthly variation, *post hoc* multiple comparisons did not distinguish among year effects.

In the three-slope model, slope aspect had the greatest effect after month. Simulation-based *post hoc* comparisons (Edwards and Berry 1987) with a 0.05 family-wise error rate differentiated between the southern and western slopes, but the northern slope could not be differentiated from either. These results indicate that the incidence of yellowjackets in traps was higher on the southern than on the western slope, whereas their incidence on the northern slope was intermediate but statistically indistinguishable from either.

The effect of elevation was also significant in both models, though on the eastern slope there were only three instead of five elevation categories. Both queens and workers were caught at 2,800 m, the highest altitude surveyed, on all four slopes. On the northern, western, and southern slopes, *post hoc* comparisons failed to detect significant differences between elevations, although the observed trend was for decreasing yellowjacket presence with increasing elevation. On the eastern slope, a simulation-based comparison showed that yellowjacket occurrence was significantly higher at the uppermost elevation (2,800 m), but it could not distinguish between the 2,650 and 2,500 m elevation categories.

Discussion

Yellowjackets were unevenly distributed both around and up the slopes of Mauna Kea, but the same seasonal capture pattern was evident on all four slopes (Figures 21.2 and 21.3). The complex patterns of abundance and occurrence among years and slopes (Figures 21.2 and 21.3) indicated that Mauna Kea yellowjacket population dynamics were governed by a non-obvious interaction between temporal (year) and spatial (slope) factors. Although the same basic occurrence pattern was present in all five years of our study, the slope-specific variation among years suggested a more complicated spatio-temporal relationship.

The interaction between year and month on all four slopes of Mauna Kea (Tables 21.1 and 21.2) suggested that the timing and extent of the increase in the incidence of yellowjackets (as represented by the month factor) could have been dependent upon weather or other factors that varied annually. The trade wind inversion layer is a common feature of the Hawaiian climate that seasonally influences temperature, moisture, and insolation (Juvik *et al.* 1993, Cao *et al.* 2007). Ground fog and insolation were putative limiting factors of yellowjackets on Haleakalā (Gambino and Loope 1992). Drier, warmer weather during spring in its native habitat in the North American Pacific Northwest seems to promote yellowjacket outbreaks, the most critical period being the initial phase of nest construction by the new queen (Akre and Reed 1981). Although rainfall, fog interception, temperature, or solar insolation may have affected yellowjacket incidence and abundance patterns in the subalpine habitat on Mauna Kea, we did not investigate potential differences in climate on the four slopes to explain, for example, why yellowjackets were more abundant and widespread on the eastern slope.

The distribution of shrub and herbaceous ground cover, which may affect the availability of preferred prey might also explain the differences in the incidence and abundance of yellowjackets on the four slopes. Pūkiawe shrubs, which were abundant on the northern and eastern slopes, may have been particularly influential in supporting large yellowjacket populations there. Yellowjacket nests were significantly more common under pūkiawe shrubs than elsewhere on Haleakalā (Gambino *et al.* 1990). Additionally, over 90% of yellowjacket foraging bouts targeted pūkiawe on Haleakalā, where yellowjackets were attracted to honeydew secreted by an endemic sap-feeding mealybug (*Pseudococcus nudus* Ferris; Homoptera: Pseudococcidae). Although we did not search for this species on Mauna Kea, *P. nudus* is present on Hawai'i Island (Nishida 2002) and there could be slope-specific variability in the abundance of this or some other prey species favored by yellowjackets. Moreover, numerous alien species have invaded Mauna Kea (Banko *et al.* 2002a), and the yellowjacket populations we studied may have been responding to variations in the availability of one or more arthropod prey species.

Another factor that might explain the interaction between slope and year and the overall distribution pattern of yellowjackets was the greater road access on the southern and western slopes. With greater road access, there is also an associated increase in human activity on these slopes.

The annual timing of yellowjacket colony development on Mauna Kea generally followed the majority of native North American populations (Akre *et al.* 1980) and it very closely followed that of high-elevation populations found on Haleakalā, Maui (Gambino 1991). Our trapping results suggested that in the spring, solitary queens emerged from hibernation, built a nest, and started producing workers. In late summer and early autumn, increased yellowjacket numbers in traps indicated that worker numbers at the nest were high (Figure 21.2). In later autumn, worker numbers in traps declined, presumably as colonies produced queens, which then mated, dispersed, and entered hibernation. Some colonies may have overwintered, such as those reported for yellowjackets in mild coastal areas in California (Duncan 1939, Visscher and Vetter 2003) and above 2,000 m elevation on Haleakalā, where there was worker activity in all months in half of the annual surveys (Nakahara and Lai 1981, Gambino *et al.* 1990). The timing of colony development on Mauna Kea is not totally in accord with other studies; Gruner and Foote (2000) found that queen abundance in Hawai'i peaked during March–May and approached zero by July. Possibly because of the higher elevation and lower temperatures, the abundance of Mauna Kea queens peaked later (June) and their decline extended later (through September). However, our worker results agreed with Gruner and Foote (2000), suggesting different colony dynamics on Mauna Kea compared to other areas of Hawai'i.

The yellowjacket is a voracious generalist arthropod predator and scavenger, known to disrupt the nutrient cycles, pollinator webs, and functions of ecosystems, particularly in island ecosystems (Akre *et al.* 1980, Bashford 2001, Beggs 2001, Hanna *et al*. 2013). However, no significant differences in arthropod communities were noted in Argentina between natural (control) areas and other areas where populations of a similar species of wasp (*V. germanica*) were experimentally reduced (Sackmann *et al.* 2008). Ecosystem-level effects of wasps may not have been observed in this instance because wasp numbers declined by only 50% over three years within a small (80 ha) continental study site. In contrast, Hanna *et al.* (2013) reported area-wide impacts to the composition of floral visitors and pollination of the dominant tree in Hawai'i when *V. pensylvanica* populations were experimentally reduced by more than 95%.

Beggs and Rees (1999) found that the survival rate of Lepidoptera larvae in New Zealand decreased with increasing *V. vulgaris* density, and during peak wasp abundance (2.7 wasps per trap per day) there was no likelihood of larvae surviving to adulthood. On Haleakalā and Mauna Loa, *V. pensylvanica* preyed heavily on Lepidoptera larvae and spiders (Araneae), and up to two-thirds of the prey items intercepted from yellowjacket workers were endemic taxa (Gambino *et al.* 1987, Gambino 1992). However, *Vespula* are not prey specialists, but instead harvest the most easily obtained arthropods on vegetation or the ground (Gambino and Loope 1992, Wilson *et al.* 2009). Results of these island studies suggest the possibility that yellowjackets on Mauna Kea could start a trophic cascade that might reduce the availability of prey for native predators and otherwise alter regional food webs.

Gambino and Loope (1992) also suggested that yellowjackets could directly compete for arthropod prey with native Hawaiian birds. Beggs and Wilson (1991) found that alien wasps (*V. germanica* and *V. vulgaris*) threatened the survival of a New Zealand parrot by competing for food. The palila is found only on Mauna Kea between 2,000 and 3,000 m elevation (Banko *et al.* 2002a, b). Lepidoptera larvae are a critical food of palila, and although their major prey, *Cydia plicata* (Walsingham; Tortricidae), are found inside māmane seed pods, the impacts of yellowjackets on the adult moth population or on other lepidopteran larvae are unknown. The palila population is concentrated on the western slope of Mauna Kea (Banko *et al.* 2013), where yellowjacket abundance and occurrence tend to be lowest. Additional studies could determine whether arthropod prey are becoming less available to palila and other native birds due to yellowjacket predation and whether there may be other ecosystem impacts. Although we have no evidence of predation on native birds by yellowjackets, Moller (1990) reported *V. germanica* attacking and killing newly hatched birds, suggesting that yellowjackets could pose a predatory threat to birds on Mauna Kea.

Dispersal in all *Vespula* species is accomplished by queens, which hibernate and emerge in the spring to start new colonies (Akre *et al.* 1980, Gambino and Loope 1992). Gambino *et al.* (1990) found a bimodal distribution of nests on Maui with one peak at 750–900 m and another at 2,550–2,700 m elevations. The maximum foraging distance of workers is unknown, but Akre *et al.* (1975) reported that workers tended to forage close to their nest; thus wasp impacts are relatively concentrated and limited mainly by the dispersal of queens. On the other hand, workers have been observed foraging at least 500 m from their nest (P. Gambino personal communication) and substantial numbers of workers were caught at the highest study sites on both Haleakalā (3,018 m; Gambino *et al.* 1990) and Mauna Loa (2,165 m; Gambino and Loope 1992). Likewise, we found high numbers in all years and slopes at our maximum elevation (2,800 m) near the tree line. Yellowjackets have been detected at Pu'u Hau 'Oki (Pacific Analytics 2000), near the summit of Mauna Kea (4,200 m). Because environmental conditions at the summit prevent the formation of yellowjacket colonies, it seems likely that individuals found in the summit region originate from near the tree line.

The occurrence and abundance of yellowjackets on Mauna Kea varied depending on the slope, year, and elevation. The only consistent pattern was the seasonal cycle of occurrence. Our results indicate several areas of yellowjacket ecology that need additional study on Mauna Kea. The first is to determine the actual impact of yellowjacket predation on native arthropod communities and the ramifications for the entire subalpine ecosystem on Mauna Kea. The second is to confirm that yellowjacket colonies overwinter above 2,200 m elevation on Mauna Kea, as they do on Mauna Loa (D. Foote, U.S. Geological Survey, personal communication). If yellowjacket colonies do overwinter on Mauna Kea, it would be useful to know the prevalence of this behavior and its implications for yellowjacket population dynamics and impacts. The detection of workers during winter months indicates the possibility of overwintering nests nearby, or possibly in pasturelands 500 m downslope and 1,500 m distant from our study site. A third research need is to identify yellowjacket nesting habitat and colony distribution on Mauna Kea to improve survey methods and develop control strategies.

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22 THREATS TO FOOD RESOURCES: ANTS

Chris Farmer, Marla Schwarzfeld, Peter T. Oboyski, David M. Pollock, John W. Slotterback, Kevin W. Brinck, Paul C. Banko

Introduction

Ants have great potential to degrade Hawaiian ecosystems by eliminating or diminishing native insect communities (Reimer 1994). Native insect communities in Hawaiʽi are particularly vulnerable because there were no ants prior to human arrival. The majority of ant species arrived within the last 100 years (Reimer *et al*. 1990). Hence, native insects have not evolved defenses against ants (Reimer *et al*. 1990). Perkins (1913) observed destruction of entire insect communities by ants in Hawaiian lowlands, and more recently, Cole *et al*. (1992) have documented impacts of ants on native insects at high elevations on Maui. There are now approximately 42 species of ants established in the Hawaiian Islands with 38 of those established on the island of Hawaiʽi (Nishida 2002). Our goal was to evaluate the threat of ants to insect communities in the dry, subalpine forests of Mauna Kea with respect to their potential impact on insect foods of palila (*Loxioides bailleui*).

Eight species of ants have been recorded from or near the southwestern slope of Mauna Kea. Wetterer *et al*. (1998) conducted surveys for ants on Mauna Kea and the Saddle Road region in 1992 and reported the following five ant species: *Cardiocondyla kagutsuchi* Terayama, *Linepithema humile* [Mayr] (Argentine ant), *Monomorium pharaonis* [Linnaeus] (pharaoh ant), *Pheidole megacephala* [Fabricius] (big-headed ant), and *Tetramorium bicarinatum* [Nylander]. *Cardiocondyla kagutsuchi* was the ant species most commonly found above 2,000 m elevation, including areas currently populated by palila (also see Chapter 18: Food Availability: Insect Surveys in the Puʻu Mali Mitigation Parcel). *Linepithema humile*, which was discovered in scattered locations above 2,000 m, is also of concern because of its aggressive foraging behavior and ability to spread rapidly in dry upland areas (Krushelnycky and Reimer 1996). Three additional species were discovered at Pōhakuloa Training Area (PTA): *Hypoponera opaciceps* [Mayr], *Tapinoma melanocephala* [Fabricius] (Oboyski 1998) and *Technomyrmex albipes* [F. Smith] (Oboyski *et al*. 2002). We conducted additional surveys to determine the distribution of ants in the upper Mauna Kea ecosystems and to assess whether potential threats to palila food resources are increasing.

Methods

Survey Area

Ant surveys extended from 1,670 to 2,870 m on the southwestern slope of Mauna Kea Volcano (summit 4,205 m) on the island of Hawaiʽi. The substrate was a mosaic of highly weathered ʽaʽā lava from multiple eruptions, ranging primarily from 4,000 to 14,000 years ago, with some exposed patches ranging from 65,000 to 250,000 years ago (Wolfe and Morris 1996). Vegetation structure was influenced by this marked substrate heterogeneity and strong gradients of elevation and aspect. Generally, surveys occurred in mixed ʽaʽaliʽi (*Dodonaea viscosa*) shrubland with *Eragrostis atropoides* grass and scattered māmane (*Sophora chrysophylla*) and naio (*Myoporum sandwicense*) trees, although ʽāheahea (*Chenopodium oahuense*) was the dominant shrub at many stations (Hess *et al.* 1999; see Chapter 24: Vegetation Structure and Composition). Frequent human activity, numerous unpaved roads, one paved east-west highway (Saddle Road), and firebreaks occurred within the survey area. We did not conduct surveys south of Saddle Road due to the danger of unexploded ordnance, military activity, and a small state park with cottages.

Sampling Design and Protocol

We conducted ant surveys in three episodes. In 1998, we re-surveyed sites surveyed by Wetterer *et al.* (1998) along existing transects, paved roads (Saddle Road), and primitive roads at various locations on the southwestern side of Mauna Kea to identify changes in ant distributions since 1992−1994. We also sampled in areas of palila habitat not included in the original surveys. During 1999−2000, we sampled ants more intensively and systematically at 587 stations along 35 transects extending upslope (east or northeast) from about 1,700 m elevation along Saddle Road to 2,900 m elevation near tree line. Transects were spaced 500 m apart along Saddle Road and narrowed to 200 m upslope. Stations were located at 200-m intervals along each transect. Surveys were conducted in the summer (June–July) and winter (November–December) of 1999 and 2000. During spring (April–May) in 2005, we revisited a subset of the 1999−2000 transects to identify changes in the distributions of ants.

In all surveys, ants were sampled using a method similar to that of Wetterer *et al.* (1998, see also Fellers and Fellers 1982) by placing approximately two grams of pureed oil-packed tuna fish on clear plastic disks (6.5 cm diameter). We also added approximately two grams of honey to the disks, thereby providing the ants with a source of sugar, protein, and lipid. Three baited disks were placed within 10 m of each station, near rocks or vegetation where foraging ants would most likely occur and the baits would retain their moisture longer. We revisited stations within two to five hours and collected representative ant specimens into 70% ethanol. To determine bait efficacy, in 2005 we intensified our surveys by searching for ants under 10–30 rocks at each station ("substrate searches").

Analysis

The maximum number of stations sampled in each of the four surveys during 1999–2000 and the 2005 survey was 546, but due to logistical constraints, only 345 stations along 33 transects were sampled in all five surveys. Therefore, we analyzed the data from these 345 stations (the primary survey), but results from other stations (the supplemental survey), which extended 120–460 m farther upslope, were used (but not shown on maps included here) to provide information about upper range limits and changes through time for each ant species.

We tested for changes in distribution by comparing the mean number of stations occupied by each species in the first four surveys (1999−2000) with the number of stations occupied in the last survey (2005) using a one-sample t-test with a sequential Bonferroni adjustment (Rice 1989). In 2005, only ants detected at baits were included in our among-years analyses; ants found only during substrate searches were excluded. To examine the spatial component of each species' distribution, we graphically compared the changes through time. Additionally, we compared the number of ant-occupied stations detected solely with baits with those detected with baits plus substrate searching over the 345 primary stations of the 2005 survey.

Results

A total of seven ant species was detected during 1999–2005 (Table 22.1). The species most frequently collected were *L. humile*, *C. kagutsuchi*, and *P. megacephala.* The other four species were much less frequently collected. *Monomorium pharaonis* was collected at low numbers in every survey (≤2% of stations) while *Cardiocondyla minutior* Forel was collected a total of five times over all stations and surveys. *Cardiocondyla emeryi* Forel and *Tetramorium simillimum*

Table 22.1. Number of stations and proportional occupancy (total n = 345) for ants on the southwestern slope of Mauna Kea, Hawai'i, in 1999, 2000, and 2005. Stations with multiple species were counted as occupied for each species. The first five columns are for baits only; the last column includes the results from our intensive rock-turning searches combined with the bait surveys at the same 345 stations.

Ant species	Summer 1999	Winter 1999	Summer 2000	Winter 2000	Spring 2005	Spring 2005 (substrate searches)
Linepithema humile	71 (21%)	111 (32%)	95 (28%)	109 (32%)	86 (25%)	105 (30%)
Pheidole megacephala	17 (3%)	18 (5%)	15 (4%)	16 (5%)	20 (6%)	21 (6%)
Cardiocondyla kagutsuchi	9 (3%)	8 (2%)	9 (3%)	17 (5%)	86 (25%)	130 (38%)
Monomorium pharaonis	3 (1%)	4 (1%)	3 (1%)	4 (1%)	8 (2%)	10 (3%)
Cardiocondyla minutior	0	1 (<1%)	1 (<1%)	0	1 (<1%)	3 (1%)
Cardiocondyla emeryi	0	0	0	0	1 (<1%)	1 (<1%)
Tetramorium simillimum	0	0	0	0	0	1 (<1%)

(F. Smith) were each collected at one station in the 2005 survey; *T. simillimum* was detected only by intensive substrate searching. We detected more than one species at the same station only 1% of the time (27 of 2,335 occasions), and usually *L. humile* was found with either *M. pharaonis* or *C. kagutsuchi*, both of which were relatively cryptic. Where species overlapped, detection and coexistence patterns were not consistent; sometimes species coexisted across multiple years, other times only one species was detected in subsequent surveys, and sometimes no species persisted. Ants were not detected at 43–71% of the stations, including many at low elevation.

Two major concentrations of *L. humile* were detected in our study area (Figure 22.1). This species was detected at a greater number of stations during the two winter surveys compared with the three spring or summer surveys (Table 22.1). Because of this seasonal cycle, the absence of winter 2005 data presumably biased our results, so we did not statistically analyze the change in distribution. A disjunct population of *L. humile* was distributed across three stations located 1,810 m upslope and northwest of the main population in 2005 (Figure 22.1). No ants were detected at these sites in summer 1999 and winter 2000; they were not sampled in the other two surveys. Based upon the 345 primary stations that were sampled in all surveys, the maximum elevation at which we detected *L. humile* was 2,340 m, a gain of 40 m from our initial survey. However, including the supplemental survey stations, we detected *L. humile* up to 2,380 m. This species coexisted at 11 stations with various combinations of four other ant species.

Pheidole megacephala was highly localized, and was found primarily in one population that remained relatively stable through time, only increasing by three stations over the course of our study (Figure 22.2). This increase in number of occupied stations from 1999–2000 to 2005 was statistically significant (Table 22.1; one-sample t-test, $t_3 = -5.42$, $P = 0.012$). We detected a new population of *P. megacephala* during our 2005 bait surveys. This population was located over 3 km from the nearest previously occupied site and was found only 260 m north of the Saddle Road near the intersection of two dirt roads. The highest initial detection in 1999 was 1,850 m elevation, and by 2005 this species had extended its range to 1,900 m.

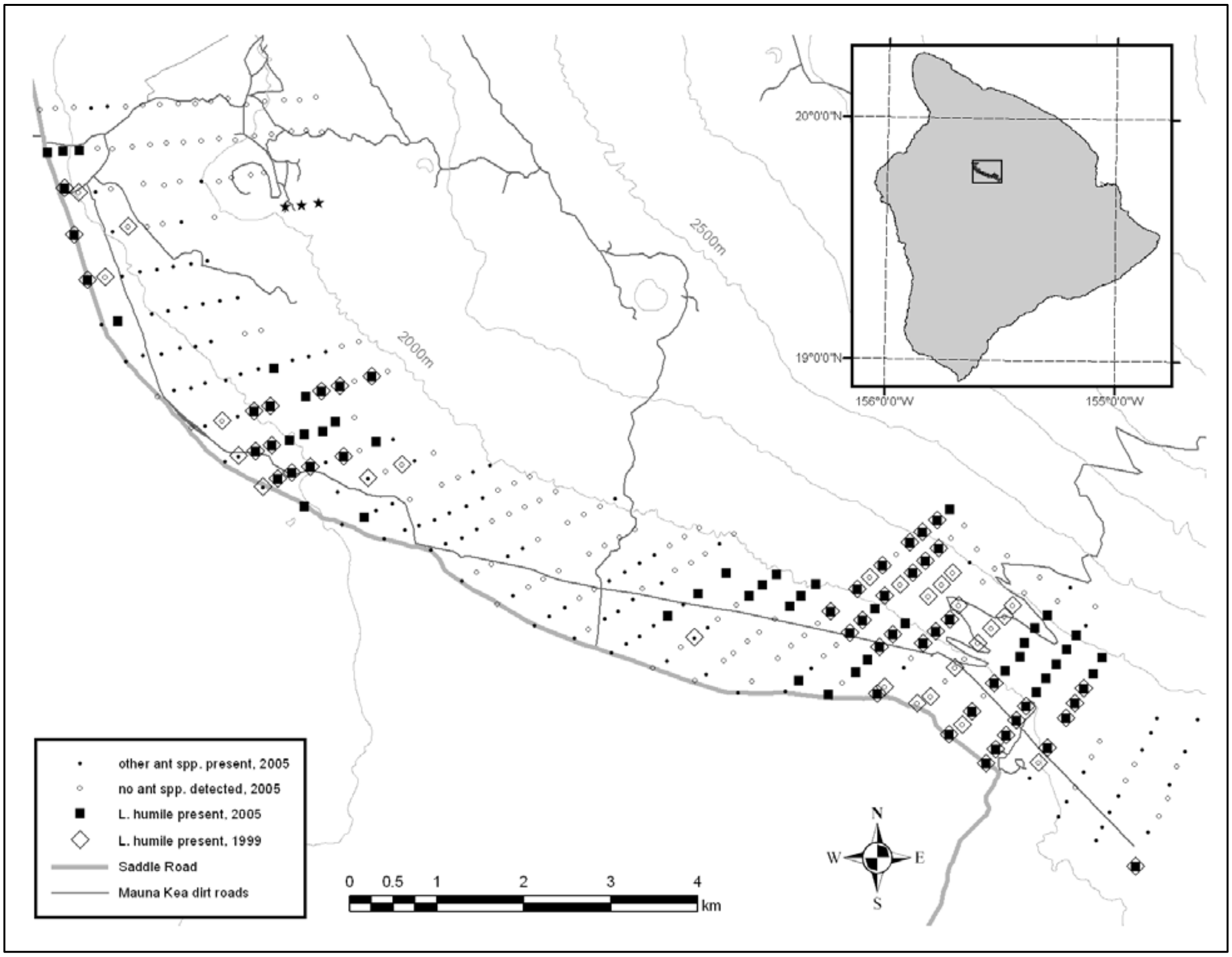

Figure 22.1. Distribution of *Linepithema humile* in summer 1999 and spring 2005 based upon detections by baiting at 345 primary stations. Three stars in the northwestern area indicate a disjunct population of *L. humile* detected only in the supplemental 2005 surveys. Inset map shows the transect locations on the southwestern slope of Mauna Kea, Hawai'i.

We detected a significant increase in the number of stations occupied by *C. kagutsuchi* in 2005 compared to 1999–2000 (Table 22.1; one-sample t-test, $t_3 = -35.9$, $P < 0.001$). *Cardiocondyla kagutsuchi* was found at numerous scattered stations, with no large continuous areas of distribution (Figure 22.3). The maximum elevation for this species increased from 2,400 m in 1999 to 2,430 m at primary stations and 2,560 m at supplemental stations in 2005 (not illustrated). This was the highest elevation at which we detected any species in any survey and was nearly 200 m above the next highest species, *L. humile*. *Cardiocondyla kagutsuchi* co-existed at 12 stations with all six other ant species found on the surveys.

Monomorium pharaonis was less widespread than the three most commonly collected species, but we detected a significant increase in range in 2005 when it was found in twice as many stations compared to 1999–2000 (Table 22.1; one-sample t-test, $t_3 = 6.8$, $P = 0.006$). Although we detected a range expansion, the maximum elevation where it was detected decreased by 10 m to 1,940 m, in 2005, using both primary and supplemental stations. The other three

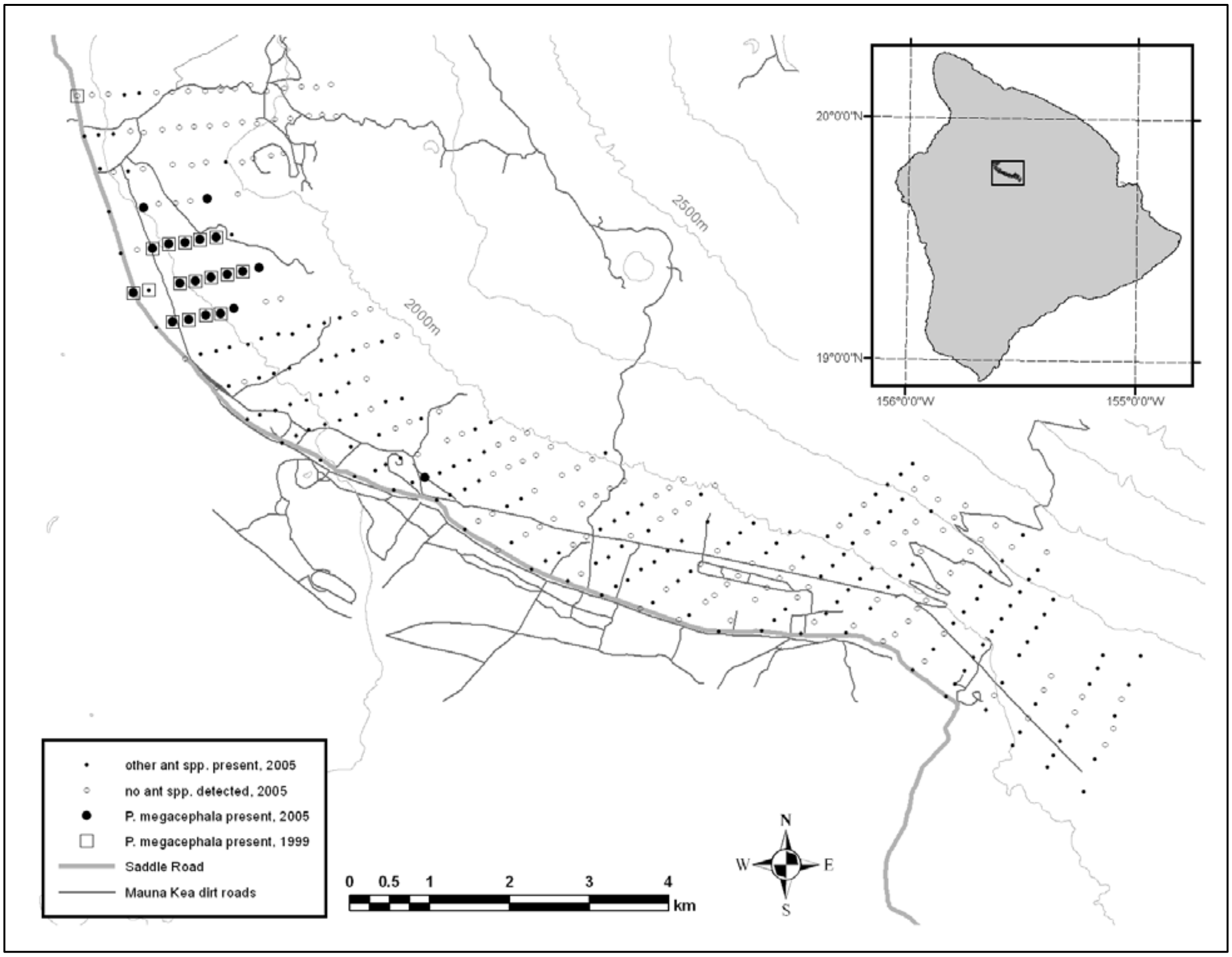

Figure 22.2. Distribution of *Pheidole megacephala* in summer 1999 and spring 2005 based upon detections by baiting at 345 primary stations. Inset map shows the transect locations on the southwestern slope of Mauna Kea, Hawai'i.

species were detected sporadically (Table 22.1). Including all stations and surveys, the maximum elevation for *C. minutior* was 2,120 m, *C. emeryi* was 1,790 m, and *T. simillimum* was 1,740 m.

Substrate searches in 2005 increased the detection of ants compared to baiting alone (Table 22.1). This resulted in an increase in the known distributions for six of the seven species, such that *C. kagutsuchi* became the most widespread species instead of *L. humile*. The results achieved by searching and baiting techniques varied by species. Searching increased the number of stations where ants were detected by 0–200%, depending on the species. Detection of the two aggressive tramp species, *L. humile* and *P. megacephala*, increased by 22% and 5% of stations, respectively. Among the more cryptic species, the widely-distributed *C. kagutsuchi* was detected at 51% more stations than baiting alone, while *C. emeryi* was not found at any additional stations. Substrate searches also increased the number of stations where more than one species of ant were detected in 2005, from nine stations with baits only to 20 stations using substrate sampling. This was particularly evident with *C. kagutsuchi* and *L. humile*. In 2005,

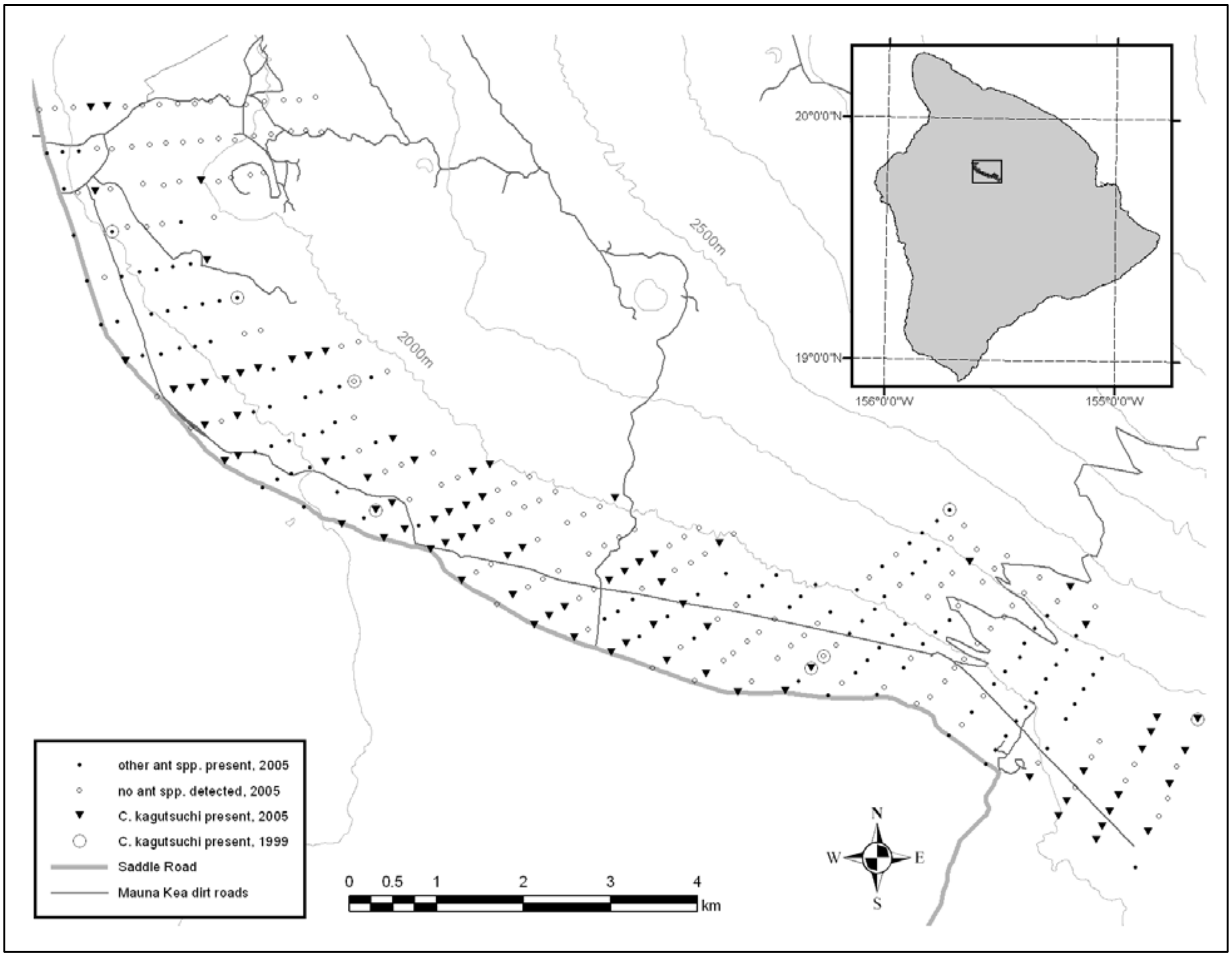

Figure 22.3. Distribution of *Cardiocondyla kagutsuchi* in summer 1999 and spring 2005 based upon detections by baiting at 345 primary stations. Inset map shows the transect locations on the southwestern slope of Mauna Kea, Hawaiʽi.

these species were detected together at three stations using baiting, but searching revealed that 13 stations were occupied by both species. Lastly, *T. simillimum* was detected only through substrate searching at a site occupied by both *L. humile* and *C. kagutsuchi*.

Discussion

We collected seven ant species in five surveys over six years, including three species (*C. minutior*, *C. emeryi*, and *T. simillimum*) not previously reported in this region. Our results indicated a significant increase in the range of three species, especially *C. kagutsuchi*. During our surveys, we detected three new species and two probable long-distance dispersal events (<600 m from roads). Multiple species coexisted at some sites for over five years, and the eventual dominant species was not always *L. humile*, which is putatively the best high-altitude competitor in dry and mesic habitats (Fluker and Beardsley 1970, Reimer 1994, Krushelnycky *et al*. 2005a). *Monomorium pharaonis*, *C. kagutsuchi*, and *C. emeryi* were all detected at sites occupied by *L. humile*. Likewise, *L. humile* did not exclude *P. megacephala* from shared sites on Mauna Kea, in contrast to earlier research in Hawaiʽi (Fluker and Beardsley 1970, Reimer 1994).

Linepithema humile and *P. megacephala* co-occur in other regions, such as Bermuda, where Lieberburg *et al*. (1975) found that *P. megacephala* could regain sites once occupied by *L. humile*. Wetterer *et al.* (2006) reanalyzed historical data from Madeira Island, a small Atlantic island 580 km off the coast of Morocco, and found that both *P. megacephala* and *L. humile* coexisted in the lowlands, and that even after 150 years these species occupied <7% of the island. These results indicate that *L. humile* invasion does not inevitably lead to the exclusion of all other ant species, and that ant distributions can be dynamic (Cooling *et al.* 2012).

Primarily as a result of substrate searching, cryptic species were detected within the interior of *L. humile*'s distribution. *Tetramorium simillimum* was collected only after intensive searching near a large colony of *L. humile*. *Monomorium pharaonis* declined to undetectable levels at two stations dominated by *L. humile* but was subsequently discovered at those same locations before expanding to an adjacent station. Our survey design limited our ability to determine the mechanisms and stability of species coexistence, but these results demonstrate that these species sometimes occur together.

Distributional patterns of the three most common species in our survey area differed, suggesting that each species' invasion had a different series of interactions with local habitat conditions or arthropod communities. *Linepithema humile* was distributed in two concentrated populations whose boundaries shifted through time; *P. megacephala* ranged within one relatively fixed area; while *C. kagutsuchi* was found scattered over the survey area. These three common species have occupied the Hawaiian Islands for various amounts of time before our surveys: *P. megacephala* for at least 129 years, *L. humile* for 68 years, and *C. kagutsuchi* possibly for 40 years (Smith 1879, Zimmerman 1941, Huddleston and Fluker 1968, Krushelnycky *et al.* 2005a). Although we do not know when each species first appeared in our survey area, the rate of spread on Mauna Kea does not seem to be a linear function of time since arrival in the islands. For example, *C. kagutsuchi* was the most recent arrival but also the most widely detected, while *P. megacephala* was the oldest invader but also the most limited in distribution. Moreover, the large gaps in ant distribution that were interspersed throughout the survey region would not likely have resulted from inadequate dispersal time. This pattern suggests that variation in vegetation structure or other habitat factors could lead to the differences in invasion rates and distribution, or species-specific response in abundance.

Linepithema humile

The tramp ant, *L. humile*, dominates the temperate regions of Hawai'i, so we expected rapid dispersal from this species (Fluker and Beardsley 1970, Reimer 1994). Bait surveys along transects by Wetterer *et al*. (1998) in 1994 suggested that *L. humile* dominated areas <2,000 m in the southeastern half of our survey area, particularly the region where the north-south unpaved road intersects with Saddle Road. They also conducted scattered pitfall trapping that revealed *L. humile* at three locations at high elevation, including one at 2,620 m. We did not observe *L. humile* on surveys or at other times above 2,400 m elevation, suggesting that the distribution of this species has contracted since 1994 (Figure 22.1). In 40% of sites surveyed in New Zealand, *L. humile* populations collapsed, resulting in a mean population survival time of 14.1 years (Cooling *et al.* 2012).

The typical seasonal pattern is that *L. humile* ants expand their range in the hotter, drier summer months, and contract in the cooler, wetter winter ones (Newell and Barber 1913, Benois 1973, Krushelnycky *et al*. 2004, Heller *et al*. 2006). On Mauna Kea, the distribution of *L. humile* contracted during the drier summer surveys (June–July) and expanded during the wetter winter surveys (November–December; Table 22.2; Western Regional Climate Center 2007), similar to the pattern in northern California where the species was more widely distributed in September compared with May during 1993–2003 (Sanders *et al*. 2001, Heller *et al*. 2006). Krushelnycky *et al*. (2004) found that abundance peaked in August–November on the upper slopes of Haleakalā, Maui. Krushelnycky *et al*. (2004, 2005b) also found that rainfall negatively affected population expansion in some areas but had no effect in other areas (<2 km distant and ≤0.5 km) higher on Haleakalā.

Table 22.2. Rainfall (mm) from Halepōhaku (Onizuka Center for International Astronomy) rain gauge, located 5.2 km east of our study region at 2,860 m elevation on Mauna Kea. Data from Western Regional Climate Center (2007). The monthly mean was calculated using data from 1950–2006.

	1998	1999	2000	2001	2002	2003	2004	2005	Monthly mean
Jan	20.3	116.8	25.4	2.5	220.2	24.1	116.1	191.8	100.6
Feb	0	213.9	0.8	98.0	119.1	0	181.6	78.7	70.4
Mar	2.3	49.5	9.9	5.1	36.6	18.3	208.5	73.7	96.8
Apr	0.3	36.1	0	20.3	67.1	43.2	137.2	23.1	65.9
May	17.3	3.3	0	11.4	168.7	0	53.3	0	30.0
June	5.1	0.0	15.2	34.5	22.9	0	6.9	0	12.0
Jul	4.1	1.5	4.3	10.7	3.3	0	7.6	0	42.9
Aug	4.8	8.1	42.9	77.7	26.7	5.1	50.8	58.9	52.3
Sep	38.1	19.6	62.7	35.1	44.7	132.1	14.0	58.4	42.1
Oct	20.3	54.4	133.6	45.0	31.0	19.1	47.0	0.0	36.9
Nov	27.4	7.6	99.1	191.0	7.6	163.3	70.6	50.8	81.8
Dec	32.3	371.9	5.1	329.2	51.1	251.5	30.5	7.6	82.5
Annual total	172.2	882.7	399.0	860.6	798.8	656.6	924.1	543.1	

Sixteen studies worldwide compiled and analyzed in Suarez *et al*. (2001) indicated that *L. humile* expanded at a rate of 0–247 m/year with a mean rate of 154 ± 21 m/year (± SE). Krushelnycky *et al*. (2005b) determined that *L. humile* advanced 18–157 m/year on Haleakalā, Maui. During 2001–2005, Krushelnycky (unpublished data) precisely mapped the change in *L. humile* distribution within 6 ha of the southeastern corner of our study area and found an overall mean spread of 1.1 m/year despite irregular expansions and contractions. *Linepithema humile* expanded at a constant rate of 60 m/yr during 2002–2005 at another site 8 km to the southeast of our study area (Krushelnycky unpublished data). These rates of movement are too slow to account for changes in station occupancy that we detected among our surveys nor the change from Wetterer *et al*.'s (1998) results in 1994. However, during our 2005 survey, we found *L. humile* within 15 m of stations where this species was previously unrecorded, so our sampling may have been too coarse-grained to detect either small colonies or small-scale expansions and contractions in distribution. Alternatively, changes in the ant's abundance, local features of the habitat (e.g., few rocks, thick vegetation), or seasonal changes in nesting behavior (Markin 1970, Heller *et al*. 2006) might have influenced our ability to detect ants at each station. The species' distribution is known to be limited by temperature, humidity, and soil moisture (Tremper 1976, Holway *et al.* 2002a, Menke and Holway 2006), so applying Hartley and Lester's (2003) degree-day model could help assess *L. humile*'s elevational limits and potential to expand further upslope on Mauna Kea.

It is difficult to predict the future distribution of *L. humile* on Mauna Kea because of uncertainty regarding the timing of its arrival on the Island of Hawai'i, but the species may not expand dramatically via budding under the current abiotic conditions. Fluker and Beardsley (1970) observed a staggered pattern of expansion by *L. humile* into the range of other alien ant species in lowland (<250 m) O'ahu. *Linepithema humile* would move 23–31 m in 10–14 days, be stationary for four-to-six months, then move again, and so expand their range 43–91 m/year. Worldwide, the Argentine ant expansion rate fluctuates among years with many areas experiencing a sigmoidal invasion rate (Suarez *et al*. 2001, Wetterer *et al*. 2006). Suarez *et al*. (2001) documented few new areas of the continental United States invaded in the first 20 years, followed by rapid expansion for approximately 30 years, then a slower increase. However, if global climate change increases temperatures or alters rainfall patterns, then *L. humile* could expand upslope on Mauna Kea (e.g., Roura-Pascual *et al.* 2004, Hijmans and Graham 2006, Jumbam *et al*. 2008). Nevertheless, dispersal mediated by human activity is a more likely prospect.

Pheidole megacephala

Previous researchers believed that *P. megacephala* would dominate the tropical lowlands (<900 m elevation), but not the more temperate highlands of Hawai'i, where it would be unlikely to compete successfully with *L. humile* (Fluker and Beardsley 1970, Reimer 1994). The species has a limited distribution on Mauna Kea compared to other invasive ant species. Wetterer *et al*. (1998) collected *P. megacephala* at one site in 1994 (1,770 m elevation; 500 m southeast of the isolated population shown in Figure 22.2), but we failed to detect it in this area. Wetterer *et al*. (1998) did not sample in the northwestern sector where we found this species. We detected a minor expansion of *P. megacephala* into four adjacent stations (mean distance between stations = 352 m) over the six-year survey period, as well as a fifth station 3 km southeast of the main population (Figure 22.2). Krushelnycky (unpublished data) documented *P. megacephala* spreading upslope at 24.4 m/year in 9.2 ha along the western edge of our main population during 2002–2004. The new elevation record (i.e., 1,900 m) documented here in addition to these other studies indicate that this species continues to expand its range (Wetterer *et al*. 1998, Krushelnycky *et al*. 2005a; Krushelnycky personal communication).

Cardiocondyla kagutsuchi

Cardiocondyla kagutsuchi is difficult to differentiate from *C. venustula* Wheeler, both of which occur in Hawai'i (Krushelnycky et al. 2005a), and it is likely that the *C. venustula* reported by Wetterer *et al.* (1998) was actually *C. kagutsuchi*. Over the six-year survey, *C. kagutsuchi* increased its range dramatically by 540 m/month between summer and winter 2000 and by 260 m/month during the following four years (Table 22.1). This range expansion may have been in response to improving habitat conditions following a severe drought in 1998 (Table 22.2), when most 'āheahea shrubs and many other plants died. If the range of *C. kagutsuchi* contracted during the drought, its rapid expansion in 2000 may indicate a greater sensitivity to changes in habitat or weather than the other species, none of which responded similarly after the 1998 drought.

Cardiocondyla species are omnivores that frequently move among nest sites. Although winged dispersal occurs during nuptial flights, new colonies typically result from budding (Heinze *et al.* 2006). However, their rapid expansion and patchy distribution (Figure 22.3) strongly suggest that nuptial flights are relatively common on Mauna Kea. Hölldobler and Wilson (1990) considered *Cardiocondyla* species "insinuators," relying upon stealth and small body size to successfully forage within the territory of more aggressive ant species. Intensive substrate searches produced more detections than did baiting, revealing it to be the most widespread species in the area (Table 22.1). Similar to Heinze *et al.*'s (2006) results, we found colonies of this non-aggressive ant throughout the study area, even in the midst of large populations of the more aggressive *L. humile* and *P. megacephala*. *Linepithema humile* were observed carrying dead *C. kagutsuchi*, but some *C. kagutsuchi* nests were within 1 m of *L. humile* nest holes. Evidence suggests that *Cardiocondyla* have an effective chemical defense against more dominant species (Creighton and Snelling 1974, Gulmahamad 1997). Relatively little is known about the effects of this species on arthropod communities, although it is generally regarded as non-threatening (Krushelnycky and Reimer 1996, Heinze *et al*. 2006). However, its rapid increase in distribution on Mauna Kea, both laterally and upslope, warrants additional monitoring and research.

Threats to Native Communities

If budding were the only means by which alien ants spread, our survey results suggest that decades would pass before populations of *L. humile*, *P. megacephala*, and *M. pharaonis* would threaten the sensitive native communities and endangered species found at higher elevations on Mauna Kea. However, both *L. humile* and *P. megacephala* were detected at stations far from their main concentrations, suggesting long-distance, jump-dispersal (Figures 22.1 and 22.2, respectively), spreading at about 10 times the average annual rate of other species we surveyed. Because the queens of both species typically disperse by budding, their long-distance dispersal was likely to have been human-assisted. Of additional concern is that *L. humile* suddenly appeared within the nesting range of the endangered palila, potentially putting at risk the birds' eggs, young, and arthropod prey. Further invasion of palila habitat seems likely because this area is traversed by roads and frequented by people.

Previous studies indicate that *M. pharaonis* and *P. megacephala* have little tolerance for cold temperatures (Creighton 1950, Reimer 1994). Therefore, it is notable that *M. pharaonis* persists at 1,940 m elevation on Mauna Kea and was found in the midst of large colonies of *L. humile* (Table 22.1). The persistence of *P. megacephala* for six years at 1,900 m elevation, well above its typical range, may indicate adaptation to the local environmental conditions.

Continued invasion of the native woodland and shrubland communities by ants could disturb native arthropod and bird communities through predation, competition, and disruption of food and pollinator webs (Holway *et al*. 2002b, Lach 2008). Although our surveys were conducted on the ground, we observed *L. humile* at the nectaries of *Sophora* flowers near Mauna Kea State Park, which indicates a potential level of threat to arboreal nectar resources and insect pollinators (Lach 2008). Human activity on Mauna Kea may increase the likelihood of ant invasion through long-distance jump-dispersal. Additional surveys to detect ant encroachment into high-elevation native communities would help managers to eradicate local invasions before they become widespread and more difficult to control. The detection of ants in future surveys would be enhanced by substrate searching as well as baiting.

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23 THREATS TO FOOD RESOURCES: PREDACIOUS GROUND BEETLE

John W. Slotterback, Paul C. Banko

Introduction

Introduced ants, parasitic wasps, predatory wasps, and predacious ground beetles (Coleoptera: Carabidae) have a combined potential that far exceed their individual potential for negatively impacting food resources of the palila (*Loxioides bailleui*) and native insect communities in Palila Critical Habitat on Mauna Kea. We examined the abundance and distribution of the introduced ground beetle, *Laemostenus complanatus* (DeJean), which is thought to have been accidentally introduced into Hawai'i in the 1940s. The first specimen of *L. complanatus* from Hawai'i was reported in 1950 from Kīpuka Puaulu on Mauna Loa (Zimmerman 1972, Leibherr and Zimmerman 2000). Additional records indicate that *L. complanatus* had established itself from Kīlauea to the Kohala Mountains by 1964, occupying habitats between 1150–2000 m elevation (Leibherr and Zimmerman 2000). Like most carabid beetles, *L. complanatus* is predacious on other insects. During daylight these beetles can be found under rocks, under mullein (*Verbascum* sp.), or beneath the loose bark of trees (Leibherr and Zimmerman 2000). At night the beetles can be seen moving on the ground or in māmane (*Sophora chrysophylla*) and naio (*Myoporum sandwicense*) trees on Mauna Kea.

Methods

We surveyed for *L. complanatus* using pitfall traps at 10 sites around Mauna Kea (Figure 23.1) in 1992, 1993, 1994, and 2002. Each site was sampled with ten, indiscriminately-placed traps arranged in a large loop for convenience. The pitfall traps consisted of 87 x 94-mm plastic conduit, a 177-ml (6 oz) plastic specimen cup, antifreeze, water, and a 150 x 144 x 10 mm wooden cover. The plastic conduit was placed so that the top was slightly below the ground surface. This served to hold the specimen cup that was placed inside so the top was level with the surface of the ground. The surrounding soil was then smoothed over the plastic conduit to produce an even transition between ground and trap. The cup was filled with 59 ml (2 oz) of a 50/50 mixture of antifreeze and water. Four small rocks were placed near the trap to elevate the wooden cover so that insects could crawl underneath while still protecting the contents of the trap from the weather, and a large rock was placed on the cover to hold it in place. The traps were collected and reset approximately every 30 days during March 1992–January 1995 and again during May–November 2002. Numbers of *L. complanatus* were pooled by site and counted to estimate the average number of beetles collected per day.

Results

We collected 39,124 specimens of *Laemostenus complanatus* during the study (Table 23.1). The sites with the highest populations were BASE and AHUM with 18,153 specimens and 17,666 specimens, respectively. The 2002 pitfall survey indicated that populations in these two areas remained higher than in other areas over the 10-year period. More beetles were collected at KEMO, PLMA, KAPE, and MANA in 2002 than they were during 1992–1995. On the other hand, trap yields were 1−3 orders of magnitude lower at POHA, AHUM, and BASE in 2002. We did not record the beetle at KANA and KALU, but we detected beetles at SKYL for the first time in 2002.

The number of beetles caught per trap-day varied both among sites and over time (Figures 23.2 and 23.3). The AHUM site yielded almost 11 beetles per day during October−November 1992, but by December 1994 the capture rate declined to less than one per day. This low capture rate continued during 2002, when the rate peaked at 0.62 in August.

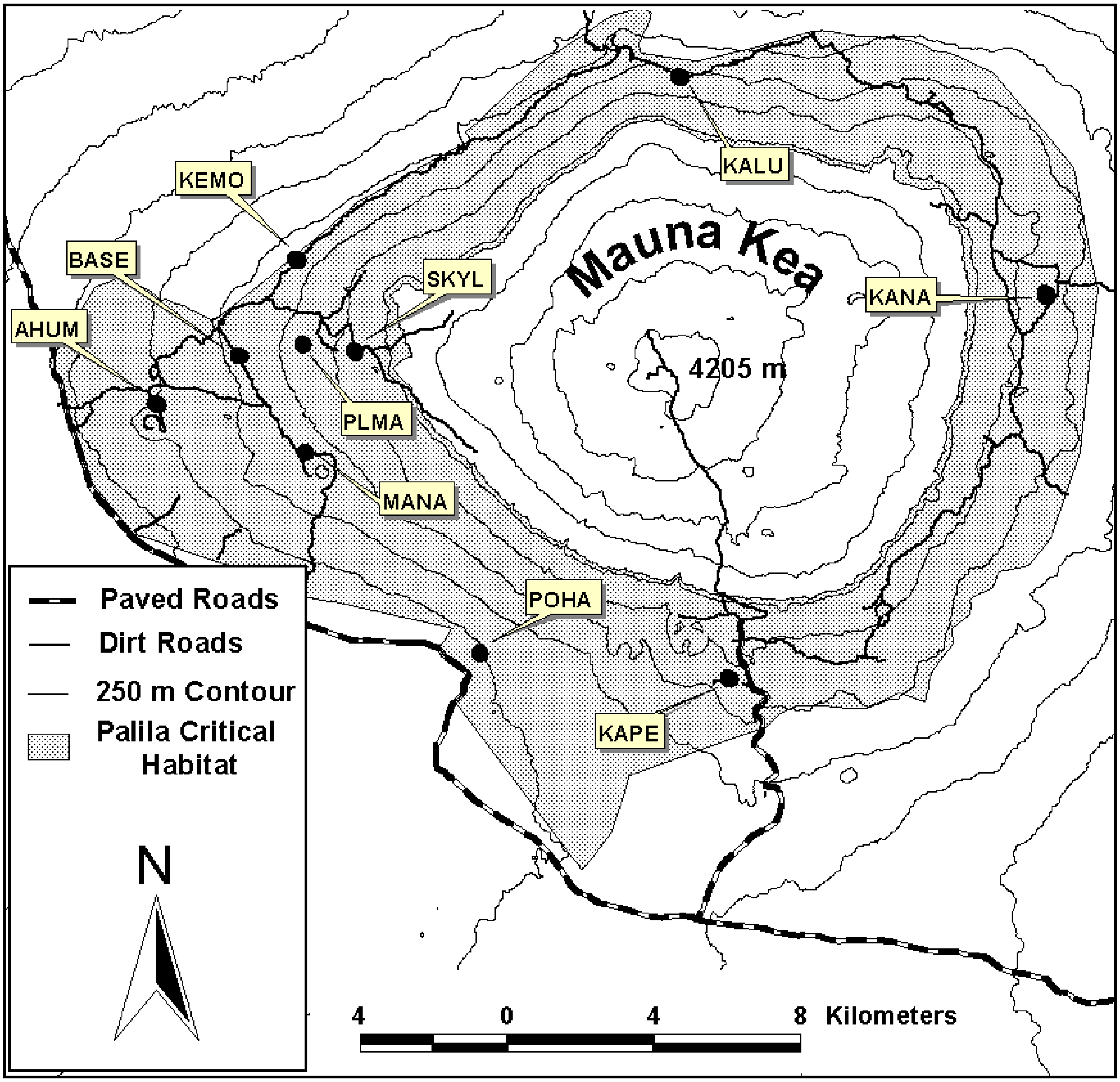

Figure 23.1. Pitfall trap sites surveyed for *Laemostenus complanatus* on Mauna Kea, Hawai'i, during 1992–1994 and 2002.

Table 23.1. Number of specimens of *Laemostenus complanatus* collected in pitfall traps on Mauna Kea, Hawai'i, during 1992−1994 and 2002. Sampling was not conducted at some sites in some years (nc = samples not collected).

Year	POHA	AHUM	KEMO	PLMA	SKYL	BASE	MANA	KANA	KAPE	KALU
1992	949	11,696	0	0	0	7,876	0	nc	nc	nc
1993	267	3,295	1	1	0	6,725	16	0	384	0
1994	68	2,355	5	1	0	3,005	1	nc	nc	nc
2002	6	320	22	363	10	547	674	0	537	0
Total	1,290	17,666	28	365	10	18,153	691	0	921	0

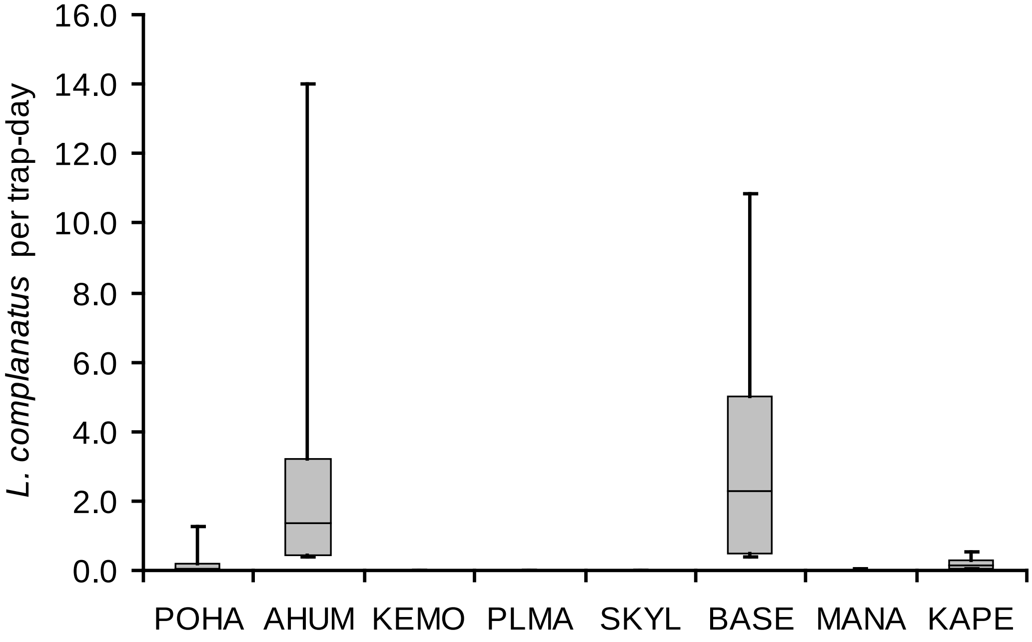

Figure 23.2. Box-and-whisker plots of *Laemostenus complanatus* captured per trap-day during 1992–1994. Whiskers represent minima and maxima of the data. Beetles were detected in very low numbers at KEMO, PLMA, SKYL, and MANA sites.

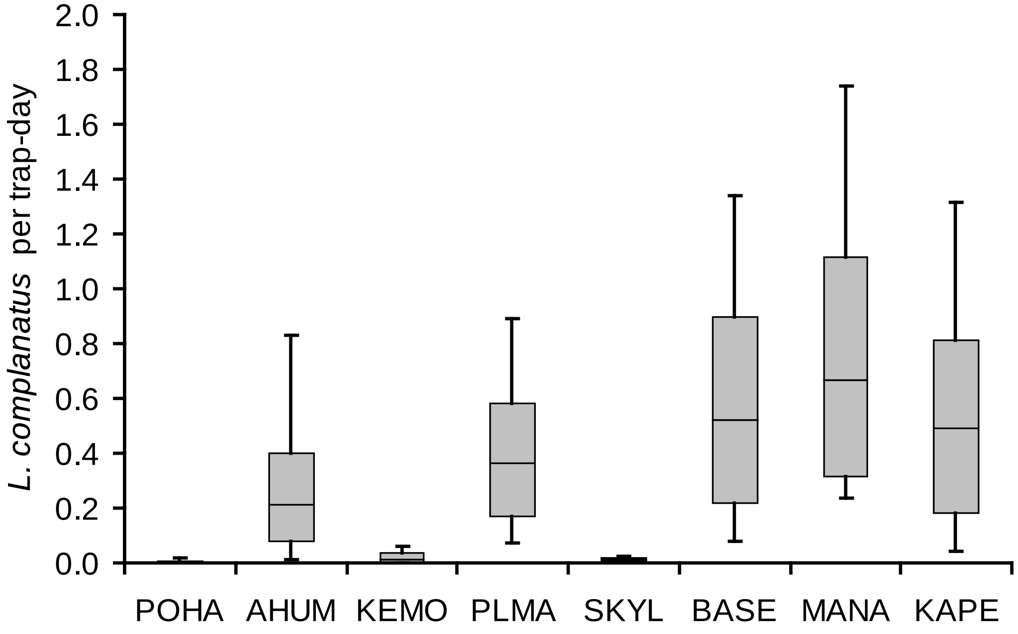

Figure 23.3. Box-and-whisker plots of *Laemostenus complanatus* captured per trap-day in 2002. Whiskers represent minima and maxima of the data. Note that the y-axis scale has changed from Figure 23.2. Compared to 1992–1995, capture rates dropped at AHUM and BASE in 2002, whereas capture rates at other sites increased slightly.

Discussion

Capture rates of *Laemostenus complanatus* dropped dramatically between 1992 and 2002, suggesting an overall decrease in the density of the beetle. Even so, the beetle's range expanded north into the MANA, KEMO, PLMA, and SKYL areas. The capture rate at POHA near Mauna Kea State Park dropped to almost zero in 2002, possibly due to the presence of the Argentine ant (*Linepithema humile* [Mayr]) at that location. Cole *et al.* (1992) found that Argentine ants caused an overall decline in arthropod abundance in a similar environment on Haleakalā, Maui. We may be able to observe these dynamics on Mauna Loa in Kīpuka Puaulu, a patch of habitat where Argentine ants have recently encroached on the edges (Peck *et al.* 2013) and *L. complanatus* is still common in the interior (D. Foote, U.S. Geological Survey, personal communication).

The impact of this introduced, generalist arthropod predator on palila food resources is unclear. Nevertheless, its expanding distribution and occasional abundance observed during our study suggest that it could add to the overall impacts of other invasive arthropod predators on food webs and trophic interactions of importance to the palila. Detailed studies of its arboreal foraging behavior could reveal important information about its potential impact on the arthropod prey of palila and other birds.

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SECTION IV: VEGETATION ECOLOGY

Preface

Palila Critical Habitat (PCH) has been degraded for over a century by a variety of introduced ungulates, but especially sheep (both feral and European mouflon) and goats. Since 1980, sheep and goat populations have been culled by public hunting and aerial shooting. This has led to widespread regeneration of māmane and other native plants, although vegetation recovery has been slow and uneven. Many species of weeds have also invaded subalpine Mauna Kea, further disturbing the native vegetation. Our goal was to characterize the vegetation to understand how palila recovery will be affected by existing and future habitat conditions and to identify areas where habitat restoration should be targeted. We classified the structure and composition of the vegetation into nine distinct associations through extensive field surveys and interpretation of satellite imagery, as described in Chapter 24, to provide a landscape overview of PCH. In Chapter 25, we describe the major results of our survey of vegetation throughout PCH during 1999–2001, including an assessment of the damage observed by ungulates. Following this effort, we conducted vegetation surveys on the lands of Ka'ohe and Pu'u Mali (see Chapter 26), which were made available for palila restoration as part of the mitigation for realigning Saddle Road through PCH.

Although we recorded the distribution of weeds during the vegetation survey of PCH (Chapter 25), we targeted 15 of the most threatening species during a separate survey in 1999. As described in Chapter 27, these species posed serious threats to PCH in terms of their potential as fire fuels, competitors with native species, smothering vines, or hosts for alien insects. We also surveyed for three noxious weeds immediately below PCH on the southwestern slope of Mauna Kea, because of the harm that could result if they invaded the core range of the palila (see Chapter 28). Because fire could have devastating consequences in PCH, we opportunistically evaluated the effects on the vegetation of a 1999 fire on the eastern slope of Mauna Kea (see Chapter 29).

Chapter 24. Vegetation Structure and Composition. Steve J. Dougill, Paul C. Banko, Steven C. Hess

Chapter 25. Vegetation Survey in Palila Critical Habitat. Steve J. Dougill, Chris Farmer, Kevin W. Brinck, Paul C. Banko

Chapter 26. Vegetation Surveys on Mitigation Parcels. Chris Farmer, Jennifer Higashino, Kalei Rapozo, Paul C. Banko

Chapter 27. Weed Survey in Palila Critical Habitat. Steve J. Dougill, Paul C. Banko

Chapter 28. Weed Survey on Southwestern Mauna Kea. Steve J. Dougill, Paul C. Banko

Chapter 29. Fire Ecology. Steve J. Dougill, Paul C. Banko

24 VEGETATION STRUCTURE AND COMPOSITION

Steve J. Dougill, Paul C. Banko, Steven C. Hess

Introduction

Remote sensing has become increasingly useful in conservation research, not only to classify vegetation communities within broad landscapes but also to investigate ecological relationships and the habitat requirements of species (Wilkie and Finn 1996, Cohen and Goward 2004). Thematic classifications of vegetation derived from satellite imagery are important for designated areas of critical habitat for endangered species (Sánchez-Azofeifa *et al*. 2003); both to identify unoccupied but potentially suitable patches and to understand how vegetation change may affect endangered species' distribution. In cases where species are strongly associated with particular aspects of plant communities, such as critical food resources, spatially explicit habitat classifications can provide valuable insights for evaluating habitat quality and carrying capacity and for identifying suitable areas in which to reintroduce species. Evaluating the response of habitat to management also may be facilitated from thematically classified imagery. Nevertheless, landscape-scale thematic classifications used to rigorously define vegetation communities are relatively uncommon, especially for tropical dry forest environments (Sánchez-Azofeifa *et al*. 2003).

We applied satellite imagery and the results of vegetation surveys to create a spatially explicit thematic classification of the critical habitat of the palila (*Loxioides bailleui*), an endangered Hawaiian honeycreeper (Fringillidae: Drepanidinae) that is restricted to dry subalpine woodland on Mauna Kea, Hawai`i (Banko *et al.* 2002). Our goal was to provide a means for exploring the palila's relationship to its habitat and for evaluating the restoration potential of its former range on Mauna Kea. The palila is highly dependent on the seeds and other food items it obtains from the endemic leguminous tree, *Sophora chrysophylla* (māmane); therefore, we were especially interested in its distribution. The subalpine plant communities of Mauna Kea have been altered and degraded by introduced ungulates, but *Sophora* and some other habitat elements began to recover after population culling began in 1980 (Scowcroft and Giffin 1983, Hess *et al*. 1999, Reddy *et al.* 2012). Our aim was to assess the potential for *Sophora* recovery in different types of habitats.

General plant community associations on Mauna Kea were described by Gagné and Cuddihy (1999) and mapped by Jacobi (1979). The vegetation maps created from aerial photo interpretation of 1976 and 1977 images at a scale of 1:24,000 (Jacobi 1979) are still widely used today for understanding gross vegetation characteristics over relatively large areas, but the resolution is insufficient to describe smaller areas and heterogeneous ecotonal plant communities. On Mauna Kea, many communities share similar species composition and are distinguished primarily by their overall structure and relative proportions of dominant species. Therefore, rigorous auxiliary data are needed in conjunction with satellite imagery to provide detailed information and to capture finer scale heterogeneity in plant communities.

Satellite imagery is also limited by scale. The LANDSAT ETM satellite records electromagnetic radiation reflected from the earth's surface at a spatial resolution of 30-m pixels. At this resolution, heterogeneous landscapes will contain conflicting information from a variety of different plant species. Nevertheless, such satellite imagery may usefully depict the general structure of plant communities and differentiate, for example, between open and dense woodlands or between savannas and open woodlands with sparse ground cover. The objectives of this research were to use LANDSAT imagery to: 1) explicitly define plant communities within set boundaries, 2) capture small-scale variability in plant community structure, 3) validate these results with a portion of reserved data, and 4) use these results to create a digital GIS layer that will help inform management within Palila Critical Habitat (PCH), identify habitats with high restoration potential, and provide a baseline for longitudinal comparisons to evaluate management actions.

Methods

We followed a sequence of four steps to construct a thematic classification of PCH. First, we used an ordination algorithm to identify structurally similar vegetation communities from a LANDSAT scene, which we termed structural landscape associations. Onto this classification we imposed boundaries of major vegetation communities derived from interpreted aerial photographs (Jacobi 1979). Within the boundaries of each vegetation community, we statistically defined species composition by summarizing data obtained from field surveys. Finally, we verified the accuracy of the resulting map using a reserved portion of the field survey data.

Using the image analyst extension of ArcView GIS 3.2 (ESRI 1999), we first carried out an unsupervised classification using the Iterative Self-Organizing Data Analysis technique, for a rectangular area of a LANDSAT ETM image from 5 February 2000. This area also contained an additional 1-km buffer around PCH which ensured that any vegetation associations confined to the lower portions of PCH would be represented in the overall classification. To balance the predictive quality of the resulting map with the number of vegetation associations that could be discriminated, we initially defined 16 classes, some of which were subsequently combined into more general, but related groups. Since the classes produced from LANDSAT ETM imagery reflected the gross physical characteristics of the area and the structure of the vegetation rather than species associations, we used vegetation maps produced from aerial photograph interpretation (Jacobi 1979) to set the boundaries between major vegetation types: woodland dominated by *Sophora*, mixed woodland of *Myoporum sandwicense* (naio) and *Sophora*, and shrubland dominated by *Leptecophylla tameiameiae* (formerly *Styphelia tameiameiae*; pūkiawe). Classes produced from the initial classification were then subdivided using these boundaries, to define the final boundaries with nine distinct vegetation associations (Appendix).

At a landscape level, we described the vegetation structure and composition for PCH within these nine vegetation associations using data from a detailed field survey (see Chapter 25: Vegetation Survey in Palila Critical Habitat). During February 1999–May 2001, we sampled 505 plots, each measuring 40 x 40 m, within PCH. To provide adequate coverage of the entire area, we systematically located the plots at 150-m intervals along 32 transects running from the upper tree line to the lower extent of woodland. Three plant communities that occurred at the edge of PCH were poorly sampled. We therefore added 38 additional plots that were randomly located within these three communities. Within each plot we counted all saplings measuring 0.2–2 m in height and compiled a complete plant species list. For all woody species greater than 2 m (hereafter, trees), we recorded each individual and characterized them as live or dead. To further assess the species composition and structure, we used a pole intercept technique (Bonham 1989). Four parallel 40-m line transects were laid out at 10-m intervals within each plot; vegetation was sampled at 1-m intervals along each transect (41 points per transect). At each sample point we placed a 2-m vertical pole and recorded each species that touched it or was projected to touch it if the pole could be extended higher. We also recorded information on vegetation at ground level and substrate characteristics at the base of the pole. Categories for the ground layer were: bare ground (rock, soil, cinder, or road) and litter, defined as any dead vegetation that was not rooted.

We summarized characteristics for sample plots that were located in areas of relatively homogeneous blocks of associations (Table 24.1). By creating a circular buffer of 30-m radius around each plot, we selected 421 plots that were surrounded by a single association that composed >75% of the buffer. The size of the buffer was determined by the addition of locational errors associated with the plot position (±5 m) and the georeferenced satellite image (±15 m). For each vegetation association we quantified the percent cover of each vegetation layer (i.e., ground, grass, shrub, and tree) and identified the most common species (those found in >50% of sample plots) that characterized the area. We also determined sapling regeneration (number of trees less than 2 m tall/ha) and tree mortality (proportion of live to dead trees) for each of the nine habitat associations. We randomly chose two-thirds of the field plots to derive the thematic classification and used the remainder to assess its accuracy (i.e., validation plots). We assessed the predictive ability of the final classification at two levels (Table 24.2). At a general level, we used percent cover to identify the dominant or co-dominant woody species for each vegetation association and identified the proportion of validation plots that contained those species. We were unable to carry out this analysis for two vegetation associations (types 1 and 8) because they lacked dominant species. At a more detailed level, we checked the accuracy of structural predictions (outlined in Table 24.1) by counting the number of validation plots whose variables fell within one standard deviation of the mean.

Building on these results, we also characterized the relative density of māmane and naio. We used an inverse distance weighted algorithm to create a deterministic interpolated surface of tree density based on values recorded in each survey plot. To increase the predictive reliability of the mapping surface, the technique was localized, and run separately in each of the nine areas. The GIS tools for this analysis were available in the spatial analyst extension of ESRI's ArcView software.

Results

Landscape Patterns

We conducted field surveys totaling >12,800 person-hours over a two-year period. The vegetation of PCH was dominated by two major structural forms: shrubland and woodland (Figure 24.1). There was a continuous band of *Leptecophylla* (*Styphelia*)-dominated shrubland above tree line. Below this was a mosaic of *Sophora* woodlands differentiated by the relative proportions of bare ground, grass, and shrubs. In actively grazed cattle pastures within PCH, open savanna of senescent *Sophora* trees and dense grasses occurred. In addition to *Sophora*-dominated woodland, *Myoporum* co-dominated much of PCH and dominated woodlands at tree line on the southwestern slope. At lower elevations, mixed *Myoporum-Sophora* woodland was less dense and patchy with predominantly native grassland, small trees, and shrubs. There was also an isolated patch of mixed woodland on a lava flow on the northeastern slope.

General Vegetation Description

We described nine vegetation themes differentiated by species composition as well as vegetation structure (Figure 24.1; Appendix). We identified two *Sophora*-dominated woodland associations differentiated by the relative proportions of grass and bare ground although species composition was very similar. We also differentiated two types of *Myoporum-Sophora* woodland based primarily on the density of canopy cover. Nevertheless, we failed to differentiate two vegetation associations that had been previously described as unique

Table 24.1. Habitat characteristics for each of the nine vegetation types obtained from survey plots (40 x 40 m). The numbers refer to mean percent cover (± SE) for each of the seven categories. We obtained cover estimates from point-intercept values from each of the survey plots. Where *Sophora* and *Myoporum* trees were found together, their canopies often overlapped; therefore the sum of their individual canopy cover was greater than the total tree cover.

		Percent cover							Percent
Habitat	*N*	Bare	Litter	Grass	Shrub	All trees	*Sophora*	*Myoporum*	live trees
Mono-dominant communities									
1	34	86.9 ± 2.1	4.9 ± 1.2	9.7 ± 1.7	1.2 ± 0.9	4.2 ± 1.3	4.1 ± 1.3	0.1 ± 0.1	94.9
2	45	76.1 ± 1.8	10.5 ± 1.2	18.2 ± 0.9	9.2 ± 1.9	3.7 ± 0.8	3.5 ± 0.8	0.2 ± 0.1	81.1
3	94	49.0 ± 1.7	17.5 ± 1.1	37.4 ± 0.8	0.9 ± 0.3	15.2 ±0.1	14.5 ± 1.1	0.8 ± 0.4	85.3
4	54	24.1 ± 2.0	22.7 ± 2.1	50.4 ± 0.4	2.4 ± 0.7	13.3 ±1.1	12.3 ± 1.0	0.9 ± 0.3	78.3
5	22	56.2 ± 3.2	15.4 ± 1.3	38.5 ± 4.7	14.3 ± 2.4	6.4 ± 1.2	6.2 ± 1.2	0	88.8
Co-dominant communities									
6	74	40.7 ± 1.6	44.0 ± 1.1	14.1 ± 1.5	11.6 ± 1.3	47.0 ± 1.5	7.9 ± 0.8	40.7 ± 1.5	83.0
7	52	41.2 ± 2.5	39.9 ± 1.9	21.6 ± 2.0	15.8 ± 2.3	31.6 ± 2.3	8.7 ± 1.0	29.8 ± 2.1	86.0
8	32	23.1 ± 2.5	30.9 ± 1.7	51.9 ± 4.0	8.7 ± 1.9	12.9 ± 2.5	3.8 ± 0.8	9.4 ± 2.0	86.0
Pasture									
9	14	14.7 ± 3.6	9.7 ± 2.2	71.8 ± 4.2	0	3.6 ± 0.8	3.5 ± 0.8	0	42.5

communities: subalpine *Chenopodium* shrubland and *Eragrostis-Panicum* grassland (Gagné and Cuddihy 1999). The spatial resolution of the imagery was insufficient to discriminate between these and neighboring mixed shrub-grassland communities.

Regeneration and Mortality

Tree regeneration varied greatly within associations (Figure 24.2). Within mixed woodland types, *Sophora* regeneration was greater than regeneration of *Myoporum* and other tree species. In actively grazed pastures on the western slope, about 60% of the standing trees were dead. Tree mortality rates were also high within *Sophora*-dominated grassy woodland (type 4); almost 25% of the standing trees were dead. There was also low sapling regeneration in this type.

Validation of the Classification

Seven of the nine habitat types were readily assigned to either a single dominant species or two co-dominant species that characterized the habitat. This classification was based on the vegetation structure in addition to the dominant species. We validated the model on a subset of the variables described in Table 24.1 and found that in 95% of the cases the defining variables of the test plots fell within an acceptable range of the reference plots (defined by the mean ± standard deviation, Table 24.2). Within the

Table 24.2. Validation of the habitat characteristics of the nine habitat types. Values are the percentage of test plots (two-thirds of total) for which habitat characteristics were correctly identified when compared with validation sites (one-third of total). For all habitat types, we investigated the agreement between the validation and the test data for: percent bare ground cover, percent grass cover, percent shrub cover, percent tree cover, and density of saplings (saplings/ha). For seven of the nine habitat types we checked the occurrence of the dominant species. We only validated the proportion of *Sophora* and *Myoporum* in co-dominant forest communities.

	Percent cover correct							
Habitat	Bare	Grass	Shrub	Tree	*Sophora*	*Myoporum*	Saplings/ha	Dominant species
Mono-dominant communities								
1	81.8	72.7	100.0	72.7	—	—	100.0	—
2	92.0	66.7	86.7	80.0	—	—	66.7	*Leptecophylla* (73.3)
3	72.4	83.3	93.3	56.6	—	—	90.0	*Sophora* (96.7)
4	72.2	83.3	94.1	61.1	—	—	94.7	*Sophora* (100)
5	87.5	62.5	50.0	100.0	—	—	100.0	*Leptecophylla* (71.4)
Co-dominant communities								
6	72.0	76.0	64.0	68.0	92.0	80.0	80.7	*Sophora* (100) *Myoporum* (100)
7	72.2	72.2	88.9	77.8	66.7	72.2	72.2	*Sophora* (100) *Myoporum* (94.4)
8	72.7	63.6	100.0	81.8	81.8	72.7	72.7	—
Pasture								
9	60.0	80.0	100.0	100.0	—	—	80.8	*Sophora* (100)

mono-dominant *Sophora* forests (types 3 and 4), the classification predicted the presence of *Sophora* trees in 96.7–100% of plots. Again, within the co-dominant forest, comprised mainly of *Myoporum* and *Sophora* trees, the classification was successful and characterized 94.4–100% of the plots correctly for both species. Although less effective in the shrubland communities, the model assigned *Leptecophylla* (*Styphelia*) to 71.4–73.3% of the plots correctly.

Relative Density of *Sophora* and *Myoporum*

The extent and density of both *Sophora* and *Myoporum* was greatest on the southwestern slope (Figure 24.3), where palila were concentrated. *Sophora* was distributed entirely around Mauna Kea but only in narrow, fragmented bands of thin coverage on the northwestern and eastern slopes (Figure 24.4). *Myoporum* was distributed almost entirely on the southwestern slope, but a small patch also occurred on the northern slope (Figure 24.5).

Discussion

This effort explicitly captured the spatial complexity and represented the most detailed description of the vegetation communities for subalpine Mauna Kea to date. By combining data obtained from satellite imagery with aerial photographs and intensive field surveys, we obtained a highly detailed thematic vegetation classification for exploring ecological relationships between the palila and its environment.

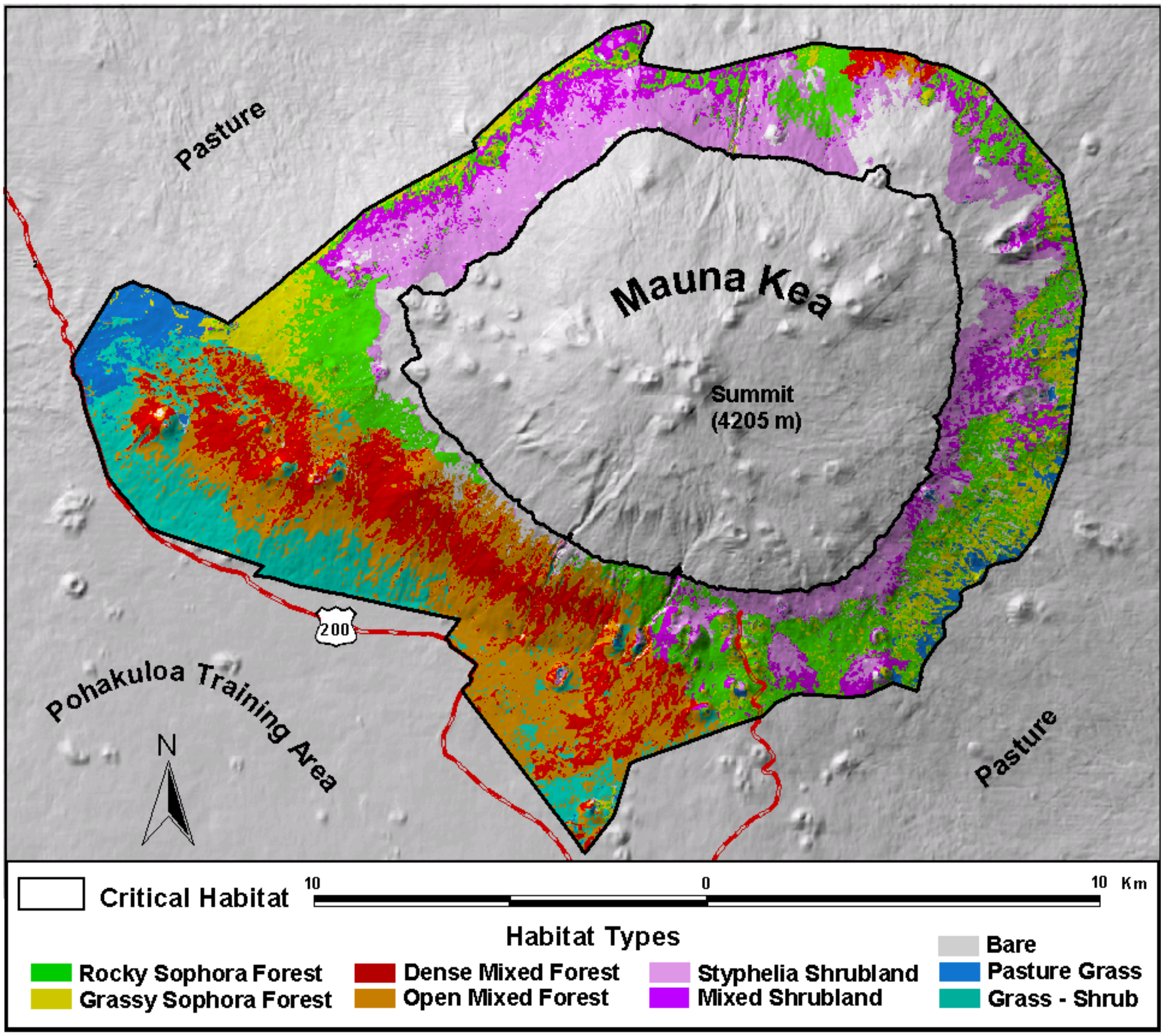

Figure 24.1. Vegetation types in Palila Critical Habitat on Mauna Kea, island of Hawai'i. Description was developed using unsupervised classification of LANDSAT satellite imagery, aerial photo interpretation to delineate major vegetation type boundaries, and 505 survey plots to sample vegetation within major type boundaries. *Styphelia* = *Leptecophylla.*

The descriptions of the vegetation communities of Mauna Kea by Gagné and Cuddihy (1999) and the vegetation maps of Jacobi (1979) provided the bases for understanding habitat structure and composition but were part of large-scale vegetation mapping efforts that covered many habitats on more than one island. The scale of our effort allows for more detailed analyses of subalpine vegetation on Mauna Kea. As in most other areas, vegetation associations on Mauna Kea are not discrete but form a continuum along gradients of elevation and rainfall. This pattern is interrupted by local disturbance events such as fire and ungulate browsing that results in a mosaic of patchy associations that may be overlooked by more general habitat descriptions.

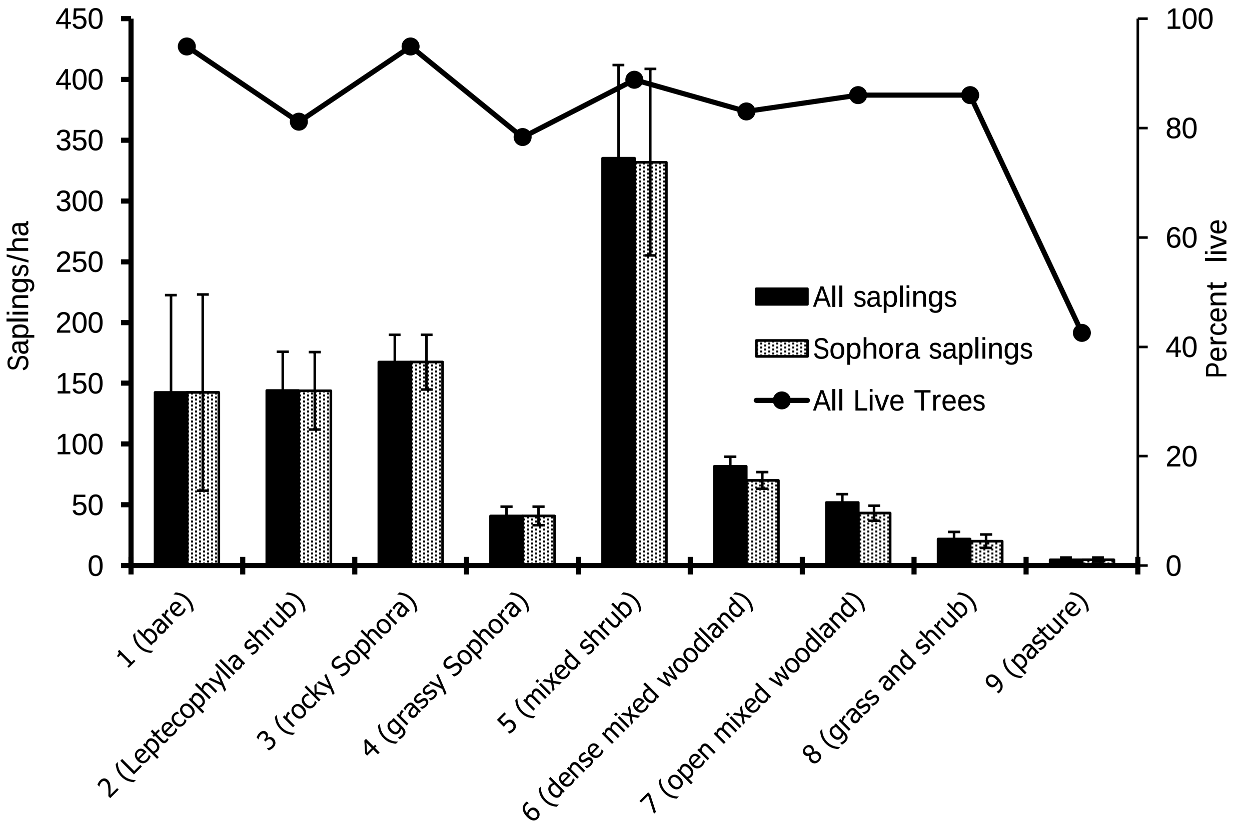

Figure 24.2. Percent of trees alive and average number of saplings per ha (± SE) in 505 plots (40 x 40 m) within nine vegetation associations on Mauna Kea, Hawai'i. Associations are: 1) bare ground, 2) *Leptecophylla* (*Styphelia*) shrubland, 3) rocky *Sophora* woodland, 4) grassy *Sophora* woodland, 5) mixed shrubland, 6) dense mixed woodland, 7) open mixed woodland, 8) grassland-shrubland, and 9) pasture grassland.

Although we were able to confirm the general boundaries among the major vegetation associations in the Jacobi (1979) aerial photo interpretation, we often found little correspondence in tree cover and some other attributes measured on our survey plots. Contributing to these differences would have been changes in tree cover since the time of the aerial photographs and dissimilarities in the methods used in the two approaches. For example, local variation is difficult to characterize at larger mapping scales, such as 2-ha units.

Additionally, the aerial photo interpretation maps were intended to assess upland forest bird habitats (Scott *et al*. 1981) and, therefore, focused on forests and wooded communities. Consequently, areas dominated by shrubland with sparse tree cover, for example, are difficult to distinguish from sparse woodlands with little shrub cover.

Our thematic classification reveals the effects of feral ungulates in PCH and provides a means for predicting changes in forest structure and composition based on *Sophora* regeneration observed in each of the nine associations. Perhaps the most dramatic change may occur in the mixed shrub community (type 5). *Sophora* regeneration was very high in this association and

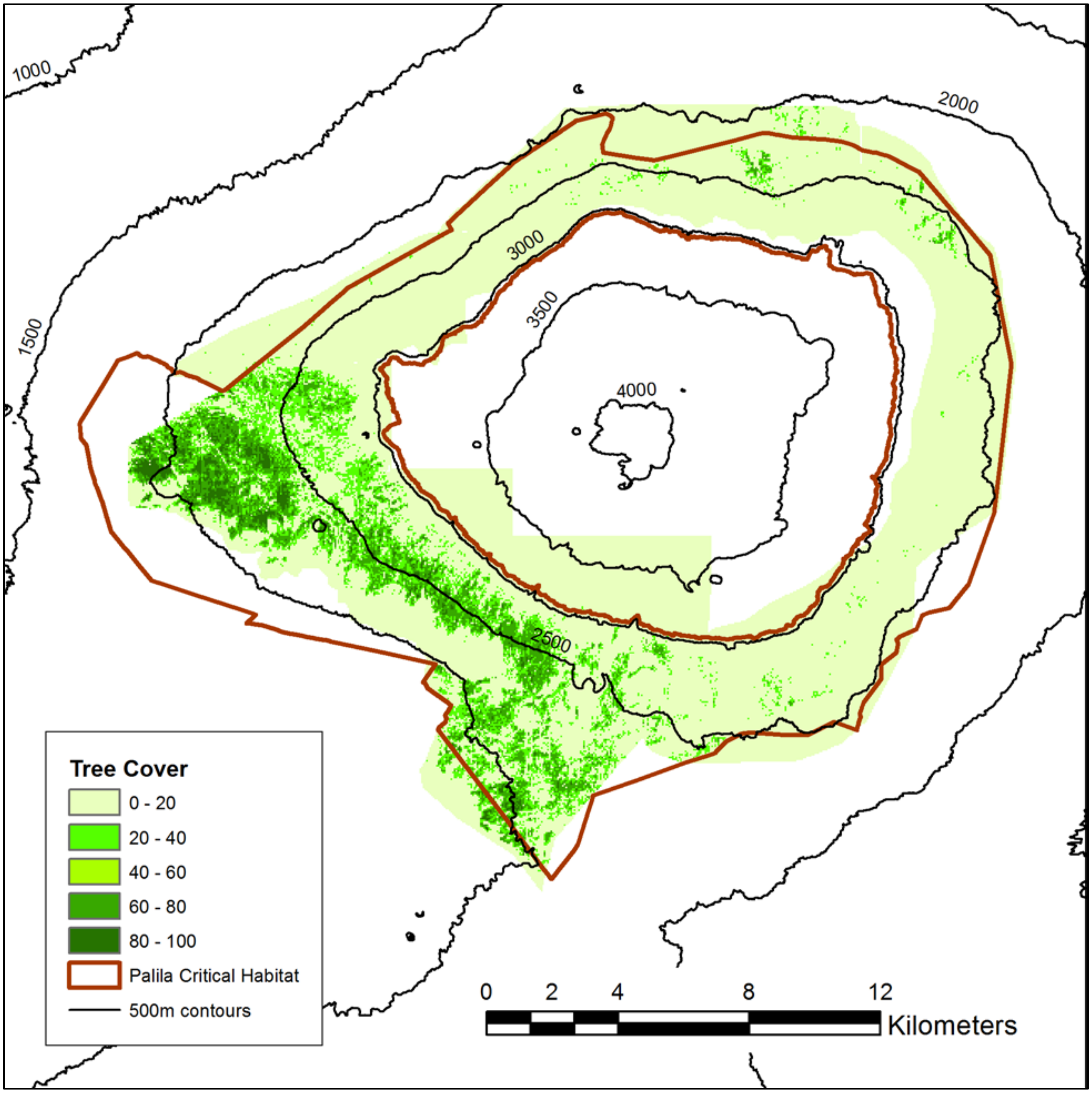

Figure 24.3. Relative cover of trees, principally *Sophora chrysophylla* and *Myoporum sandwicense*, in Palila Critical Habitat, Mauna Kea, Hawai`i.

the density of *Sophora* is likely to continue to increase if herbivores are eliminated or maintained at low levels. Recovery of this habitat would provide a habitat corridor between woodlands on the western and northern slopes of Mauna Kea. Palila are currently restricted to the western slope where they are at risk from a catastrophic event such as a large wildland fire (Thaxton and Jacobi 2009).

Sophora regeneration also was high in bare regions (type 1), where long-term sheep browsing has been especially severe at the tree line (Scowcroft and Giffin 1983). Regeneration near tree

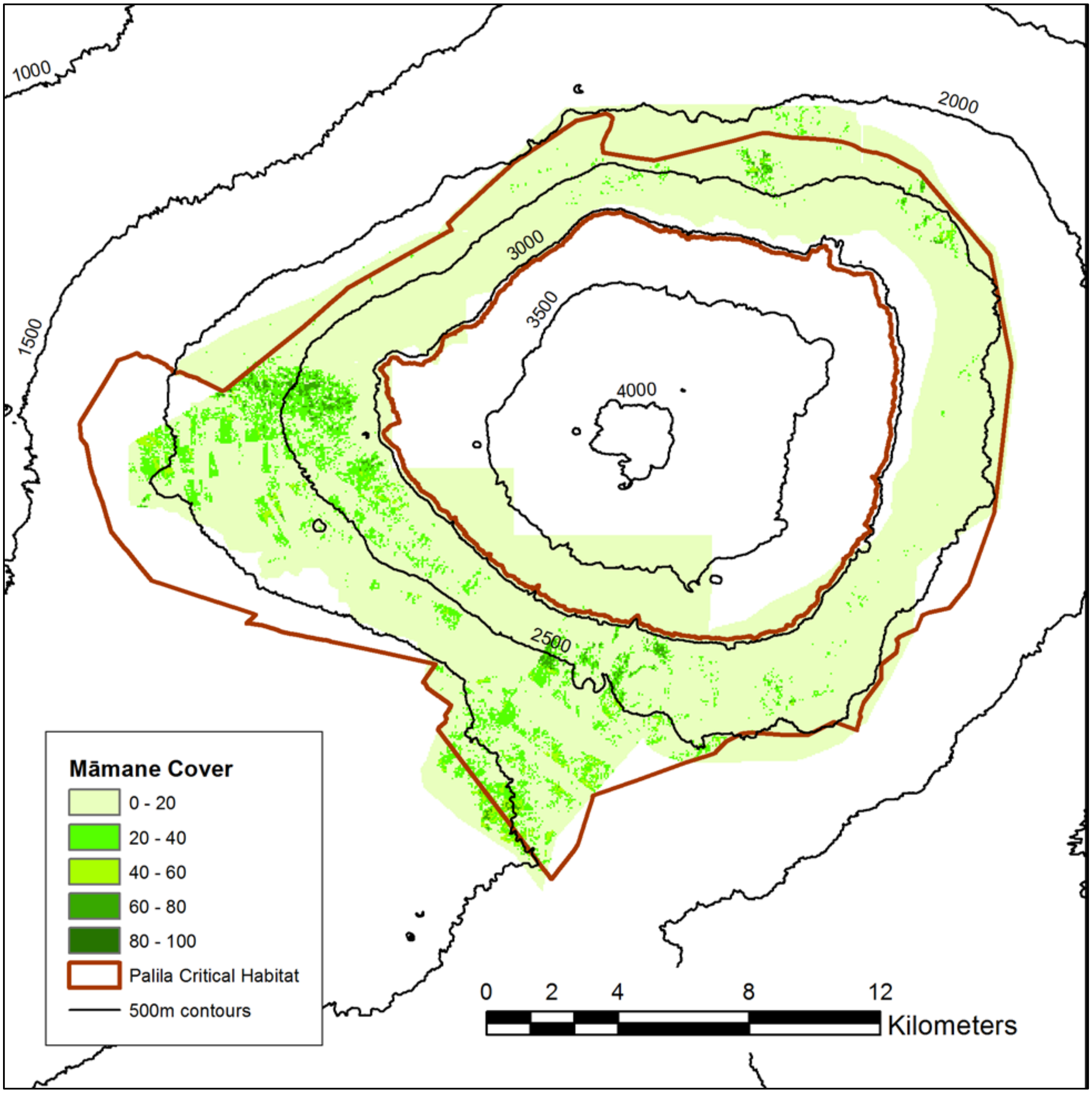

Figure 24.4. Relative cover of *Sophora chrysophylla* (māmane) in Palila Critical Habitat, Mauna Kea, Hawai'i.

line was mostly confined to rocky ridges and was lacking in large expanses of cinder and ash, possibly because rocky cracks create microclimates where young trees can become established.

In addition to the recovery of *Sophora*-dominated woodlands, *Sophora* may also become the dominant woody species in the mixed woodlands at lower elevations. We found that *Sophora* regeneration was also much greater than regeneration of *Myoporum* in co-dominant woodlands (Hess *et al.* 1999). This may be due to a reduction in preferential browse on *Sophora* by feral herbivores (Giffin 1976, 1981; Scowcroft and Sakai 1983). With the elimination of alien

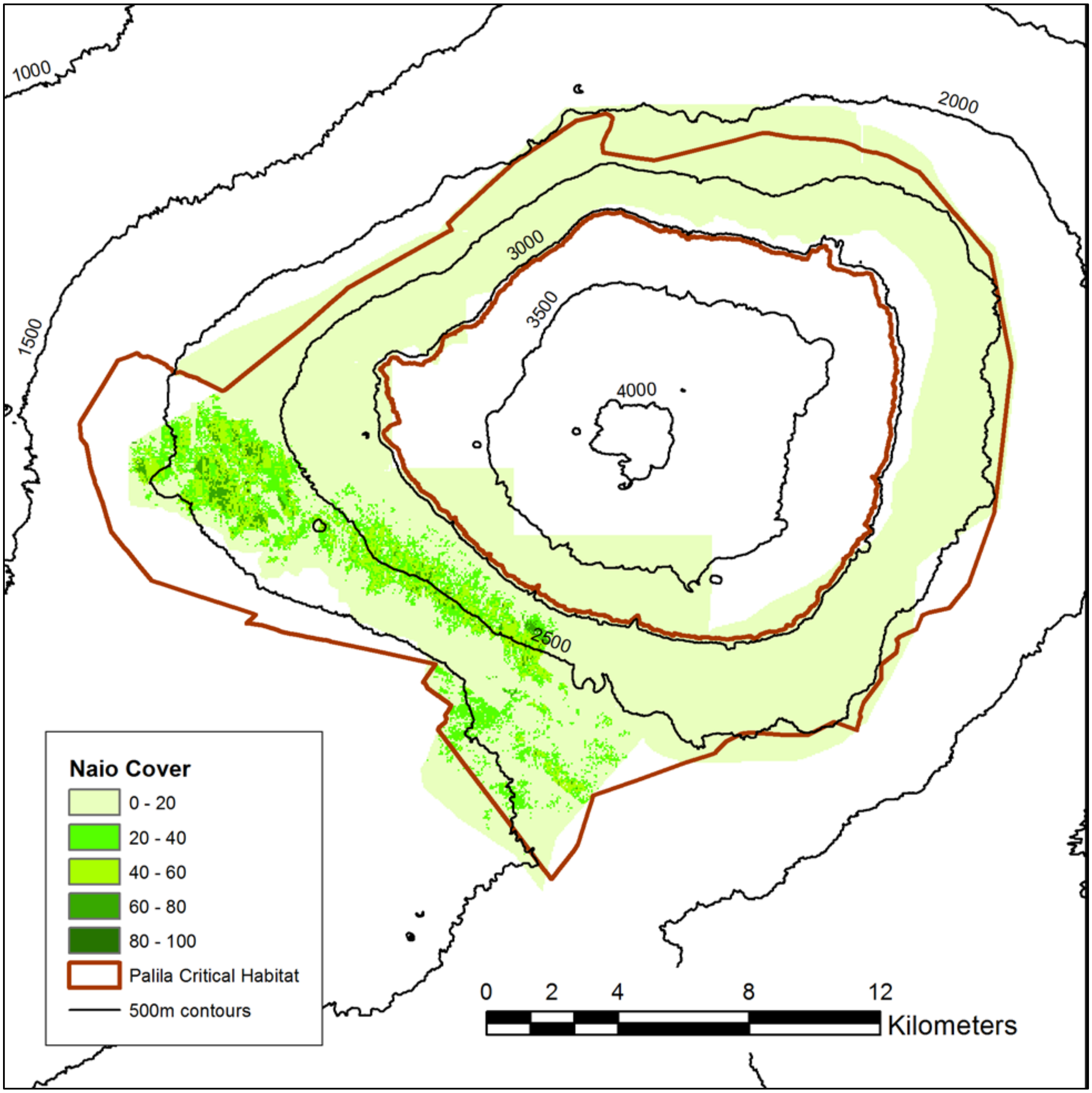

Figure 24.5. Relative cover of *Myoporum sandwicense* (naio) in Palila Critical Habitat, Mauna Kea, Hawaiʻi.

browsers, the lower western slope will likely become dominated by *Sophora*, offering palila improved habitat.

On the other hand, some areas of heavily-browsed habitat are recovering poorly. Tree mortality was high and *Sophora* regeneration poor in grassy *Sophora*-dominated woodland. A negative relationship between *Sophora* regeneration and invasive alien grass cover has been previously established (Williams 1994, Hess *et al*. 1999), but long-term browsing has been the chief cause of habitat degradation (Scowcroft 1983). In the pasture grasslands (type 9) that have been leased for cattle grazing, standing dead trees were more common than live ones and regeneration was extremely low.

Our spatially explicit thematic classification of vegetation provides a baseline for longitudinal comparisons to evaluate the effect of management strategies such as the eradication of browsers. We expect vegetation on Mauna Kea to be highly dynamic throughout this recovery phase with recovery occurring rapidly in some regions and vegetation associations and more slowly in others. Species dominance may change, alien plants may continue to invade, and ecosystem properties may change over time (D'Antonio and Vitousek 1992).

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Appendix. Structural Landscape Associations

Structural landscape associations derived from ordination of a LANDSAT thematic classification of Palila Critical Habitat (PCH) on Mauna Kea, Hawai'i. Following a brief description of each vegetation association, the most common species are listed (i.e., those species occurring in >50% of survey plots). An * indicates an alien plant species. The general life form is also added: F = fern; G = grass; H = herb; S = shrub; T = tree. Refer to Table 24.1 for a summary of vegetation characteristics for each of the nine associations including: 1) percent of bare ground cover and percent of dead, vegetative litter; 2) grass cover; 3) shrub cover; and 4) tree cover.

1. Bare, 9.5% of PCH: Generally found close to tree line or above and consisting of mostly bare, rocky ground (87%) but with low cover (<5%) of remnant native trees in some areas.

**Heterotheca grandiflora* (H)
**Hypochoeris radicata* (H)
Pellaea ternifolia (F)
**Rhytidosperma penicillatum* (G)
**Rumex acetosella* (H)
Sophora chrysophylla (T)
**Verbascum thapsus* (H)

2. *Leptecophylla* (*Styphelia*) shrubland, 18.1% of PCH: Open (>75%) shrubland generally found above tree line but also on rocky lava flows on the southern slope.

**Dactylis glomerata* (G)
**Holcus lanatus* (G)
**Hypochoeris radicata* (H)
Leptecophylla (*Styphelia*) *tameiameiae* (S)
**Rhytidosperma penicillatum* (G)
Sophora chrysophylla (T)

3. Rocky *Sophora* woodland, 16.4% of PCH: Open woodland dominated by *Sophora* trees separated by bare ground (49%) and extensive, mostly alien grass cover (32%). More common at high elevations but patches also found throughout the area.

**Anthoxanthum odoratum* (G)
**Dactylis glomerata* (G)
**Holcus lanatus* (G)
**Rhytidosperma penicillatum* (G)
**Rumex acetosella* (H)
Sophora chrysophylla (T)
Trisetum glomeratum (G)
**Verbascum thapsus* (H)

4. Grassy *Sophora* woodland, 7.6% of PCH: Similar in many ways to rocky *Sophora* woodland (type 3), but characterized by less exposed bare ground (24%) and more alien grass cover (46%). Forming an almost solid block at mid elevations on the western slope but distributed in

patches throughout PCH. At lower elevations, often occurring as a mosaic with vegetation association types 3 or 9.

**Anthoxanthum odoratum* (G)
**Dactylis glomerata* (G)
**Holcus lanatus* (G)
Sophora chrysophylla (T)
**Verbascum thapsus* (H)

5. Mixed shrubland, 7.7% of PCH: Grading into rocky *Leptecophylla* (*Styphelia*) shrubland (type 2), but differentiated by greater shrub cover (14%), twice the tree cover (7%) and greater grass cover. Generally occurring at the interface between type 2 and rocky *Sophora*-dominated woodland (type 3).

**Anthoxanthum odoratum* (G)
Asplenium adiantum-nigrum (F)
Asplenium trichomanes (F)
**Dactylis glomerata* (G)
Deschampsia nubigena (G)
**Holcus lanatus* (G)
**Hypochoeris radicata* (H)
Leptecophylla (*Styphelia*) *tameiameiae* (S)
Pellaea ternifolia (F)
**Rhytidosperma penicillatum* (G)
**Rumex acetosella* (H)
Sophora chrysophylla (T)
**Verbascum thapsus* (H)

6. Dense mixed woodland, 11.1% of PCH: Dense tree cover (47%), dominated by *Myoporum sandwicense* and *Sophora chrysophylla*. Native shrub layer common (12% cover) in areas with little ground cover (85%). Found at mid elevations on the western and southwestern slopes in an almost continuous band, bordered above and below by more open woodlands. An additional patch also found on the lower, northern slope but with no evidence of remnants of similar habitat in between.

Chenopodium oahuense (S)
**Dactylis glomerata* (G)
Dodonaea viscosa (S)
Myoporum sandwicense (T)
**Rhytidosperma penicillatum* (G)
Sophora chrysophylla (T)

7. Open mixed woodland, 16.7% of PCH: Similar to dense mixed woodland (type 6) but tree cover less dense (32%) and often co-dominated by *Myoporum* and *Sophora*. Native shrub layer common (16% cover) but little ground cover under trees (81%). Abundant at mid and low elevations on the western slope and grading into type 6 or more open grassland-shrubland (type 8).

Chenopodium oahuense (S)
**Dactylis glomerata* (G)
Myoporum sandwicense (T)
**Rhytidosperma penicillatum* (G)
Sophora chrysophylla (T)

8. Grassland-shrubland, 9.0% of PCH: Found mainly at lower elevation on the western slope, below open mixed woodland (type 7). Characterized by high grass cover (52%) and patchy shrub (9%) and tree cover (13%).

**Centaurium erythraea* (H)
**Dactylis glomerata* (G)
Dodonaea viscosa (S)
Eragrostis atropioides (G)
**Heterotheca grandiflora* (H)
**Lepidium africanum* (H)
Myoporum sandwicense (T)
**Senecio madagascariensis* (H)
Sophora chrysophylla (T)
**Verbascum thapsus* (H)

9. Pasture grassland, 3.9% of PCH: Former native forest transformed to open or wooded pasture by cattle grazing; mainly on lower western slope but small area also on lower eastern slope. Low tree cover (<4%) with >50% of trees dead (57%). Ground cover mainly grass (72%) or highly disturbed (15%).

**Cenchrus clandestinus* (G)
**Dactylis glomerata* (G)
**Holcus lanatus* (G)
**Medicago lupulina* (H)
**Plantago lanceolata* (H)
Sophora chrysophylla (T)

25 VEGETATION SURVEY IN PALILA CRITICAL HABITAT

Steve J. Dougill, Chris Farmer, Kevin W. Brinck, Paul C. Banko

Introduction

The endangered palila (*Loxioides bailleui*) is restricted to the subalpine forests of western Mauna Kea because of its reliance on high densities of māmane (*Sophora chrysophylla*) trees for food and its strong site tenacity (Scott *et al*. 1984, Fancy *et al*. 1993, Banko *et al.* 2009). The habitat of the palila has been degraded throughout its historic range, predominantly in the last two centuries by introduced feral ungulates (Hartt and Neal 1940, Warner 1960, Scowcroft and Sakai 1983, Banko *et al.* 2013), particularly sheep (*Ovis aries* and *O. gmelin musimon*), cattle (*Bos taurus*), and goats (*Capra hircus*). Alien browsers were reduced to low numbers during the 1930–1940s and again during the 1980–1990s (Pratt *et al*. 1997, Banko *et al.* 2009). Māmane regeneration in Palila Critical Habitat (PCH) proliferated following both episodes of ungulate control (Scowcroft and Sakai 1983, Scowcroft and Conrad 1988, Hess *et al*. 1999, Reddy *et al.* 2012).

Alien plant species have also invaded Mauna Kea, encouraged in part by the disturbance caused by introduced ungulates (Hess *et al.* 1999). The proliferation of weeds has altered the structure and composition of the forest, and grasses and other species have increased the threat of fire by supplying additional fine fuels (Thaxton and Jacobi 2009). Invasive cape ivy (*Delairea odorata*) overgrows māmane and may reduce its vigor and productivity. Gorse (*Ulex europaeus*) is spreading on the eastern slope of Mauna Kea and likely will invade areas occupied by palila unless control measures are developed. The dense cover formed by some alien grasses may also inhibit māmane and other native plant regeneration (Scowcroft and Sakai 1983, Hess *et al*. 1999). Changes to māmane forests by invasive alien plants could be detrimental to palila survival and productivity. The potential for increased fire frequency and intensity and for reduced māmane regeneration and vigor are major management concerns.

Palila has historically inhabited only the island of Hawaiʽi, ranging from the dry mixed forests on the volcanoes of Mauna Loa and Hualālai, northeast across the intermontane plateau in the interior of the island, to the subalpine forests of Mauna Kea (Pratt *et al*. 1997, Banko *et al.* 2002a), closely matching the range of māmane. Palila have become restricted to a small area of dry forest on Mauna Kea between 1,500–3,000 m elevation (Camp and Banko 2012, Banko *et al.* 2013). This subalpine woodland is dominated by two endemic tree species: māmane in the upper elevations and naio (*Myoporum sandwicense*) below. The forest is also home to a number of other native tree species that range from rare to locally common: koa (*Acacia koa*), ‘iliahi (*Santalum paniculatum*), pilo (*Coprosma montana*), ʽakoko (*Euphorbia olowaluana*), and naʽenaʽe (*Dubautia arborea*). The forest understory reflects local soil and climate conditions and the intensity of ungulate damage (Hess *et al.* 1999, Reddy *et al.* 2012). Although native grasses and shrubs are still abundant in some areas, alien grasses and herbs now dominate the ground cover over much of the mountain (Hess *et al*. 1999, Thaxton and Jacobi 2009).

Hartt and Neal (1940) provided the first ecological description of the subalpine forests and alpine scrub communities of Mauna Kea. The vegetation of this area was first mapped by Ripperton and Hosaka (1942) at a scale of 1:1.5 million, providing a generalized overview of potential vegetation zones for all the main islands based on existing vegetation, climatic patterns, and topography (Jacobi 1989). Building on this early work, Hawaiian vegetation has been classified in a variety of environmental zonation schemes, including Lamoureux (1983), Hawai‘i Natural Heritage Program of The Nature Conservancy (1985), Cuddihy and Stone (1990), and Gagné and Cuddihy (1999).

In addition to the zonation approach, a transect approach (Mueller-Dombois and Fosberg 1998) has been used as the core technique to establish a framework for field research (Mueller-Dombois and Krajinia 1968; Mueller-Dombois *et al*. 1981; Kitayama and Mueller-Dombois 1992, 1994a, 1994b). The transect approach has also been used widely to map vegetation communities at larger, more detailed scales (Jacobi 1978, 1985, 1990), as well as to assess changes in principal vegetation types (Kitayama and Mueller-Dombois 1995).

Building on these studies, we used a transect approach to characterize the floristic structure and composition of the subalpine forests of Mauna Kea. We utilized the framework from the vegetation surveys associated with the Hawai‘i Forest Bird Survey (HFBS), in which point locations were sampled along transects (Scott *et al*. 1981). Information collected during HFBSs related the abundance of non-native and native forest birds to vegetation structure and composition, substrate characteristics, and phenology of selected plant species. Understanding and characterizing the vegetation communities of Mauna Kea are critical steps in designing restoration strategies for the palila and its habitat. Our survey described the subalpine vegetation to better understand palila and other forest birds, mammalian predators of forest birds, ungulates and forest recovery, and insect food resources.

Our primary goal was to determine the distributions of all native and alien plant species in the subalpine forests of Mauna Kea, thereby updating the study by Jacobi (1979) and providing a more detailed baseline to monitor changes in the vegetation. Distributions of palila and other forest birds have been linked with habitat factors such as the density of mature māmane trees (Scott *et al*. 1986). Hess *et al*. (2001) found that palila track the seasonal abundance of māmane pods. The distribution and phenology of māmane and resources associated with māmane strongly influence the distribution of palila (Banko *et al.* 2002b) and can be used to predict habitat suitability for palila and identify habitat gaps that inhibit palila range expansion. Also, determining forest stand composition, recruitment, and productivity from measurements of māmane by size class could help determine spatial and temporal patterns in the availability of palila food resources (Banko *et al*. 2002b).

Although there is a long history of ungulate impacts in PCH (Hess and Banko 2011), information is needed about the frequency of browse damage and the recruitment of māmane trees and other species following efforts to cull ungulate populations since 1980. Also needed is information on the status of alien species such as cape ivy and banana poka (*Passiflora tarminiana*), which could become serious pests when released from grazing pressure (LaRosa 1992, Scowcroft and Conrad 1992), and the distributions of naturalized grasses that inhibit the regeneration of māmane seedlings (Williams 1994). Jacobi and Warshauer (1992) predicted that two important naturalized weeds, cape ivy and fountain grass (*Cenchrus setaceus*), would increase their range dramatically.

Information about other threats to palila or their habitat can also be related to results of vegetation studies. Rats (*Rattus rattus*), cats (*Felis catus*), mongoose (*Herpestes auropunctatus*), and pueo (*Asio flammeus sandwichensis*) are predators of palila and other forest birds in Hawai‘i (Tomich 1986; Amarasekare 1993; Banko *et al.* 2002a, 2009; Lindsey *et al.* 2009). When related to information on predator habitat use patterns, data on the distribution of vegetation can help guide predator control efforts. Additionally, arthropod habitat associations can be related to the results of vegetation surveys to predict the future distributions of problem species, such as ants, predacious wasps, and parasitic wasps and flies, as well as sensitive native pollinators, such as yellow-faced bees (*Hylaeus* spp.), and insects that are eaten by palila.

Methods

We collected plant specimens from the subalpine areas of Mauna Kea during early November 1998. When new plant species were encountered during the course of the survey, they were added to this collection. Plant specimens were pressed and labeled in the field. After drying, the specimens were mounted on herbarium sheets (stored at U.S. Geological Survey, Pacific Island Ecosystems Research Center). Linda Pratt (botanist, U.S. Geological Survey, Pacific Island Ecosystems Research Center) confirmed all identifications. Specimens were then photocopied, and a short identification guide was produced to aid in field identification. The specimens and additional photographs of the species were also digitally scanned to ensure a permanent, high quality color record of their images that can be shared easily with other interested parties.

We sampled the vegetation and structure on 504 study plots, distributed across 167.5 km^2 of subalpine forest habitat at high elevation (2,601−3,000 m), mid elevation (2,201−2,600 m), and low elevation (1,800−2,200 m) between February 1999–May 2001. Limited data were collected from the degraded forest below the Mauna Kea Forest Reserve. We located plots along transects extending from the upper tree line to the lower extent of the forest. The 17 original HFBS transects (transects 101 to 117; Scott *et al*. 1984) and 14 additional transects added during 1997−1998 (Johnson *et al*. 2006) provided systematic coverage of the entire mountain (Figure 25.1). We sampled at stations spaced at 150-m intervals along each transect to allow for comparisons with earlier estimates of vegetation composition and structure (Jacobi 1979, Scott *et al*. 1984).

The center of each study plot was located by a random distance (0–40 m) on a random bearing (1–360 degrees) from each station. The transect station was not used as the center of the study plot because of the possible effects of trampling and disturbance along the transect. In addition, because the transect station may have been flagged on a nearby tree for convenience, and not at the true point, tree density calculations could be slightly biased. A 40 x 40 m study plot was established with the sides oriented along the four cardinal directions (Figure 25.2).

Plots were marked and UTMs recorded from a GPS to enable future monitoring. We conducted four separate surveys within each study plot. Pole intercept was used to assess vegetation composition and structure. In addition, we characterized trees (woody species ≥2 m tall) and the shrub layer (woody species <2 m tall). We described the general characteristics of the plot, noted its slope and aspect, and completed a comprehensive plant species list. Photo documentation was obtained for a sample of the plots.

Pole Intercept

Four parallel 40-m line transects were laid out at 10-m intervals within each plot (Figure 25.2). Vegetation was sampled at 1-m intervals along each transect (41 points per transect). At each sample point, a 2-m pole was placed vertically, and we recorded any species touching the pole in three height strata (0–0.5 m, 0.5–1 m, 1–2 m); we recorded species that were predicted to touch the pole in the fourth stratum (>2 m; Bonham 1989). When a tree limb arched over the transect, the pole was placed immediately above the sample point, and its trajectory was projected to the ground point. A species touching the pole on multiple occasions within a single

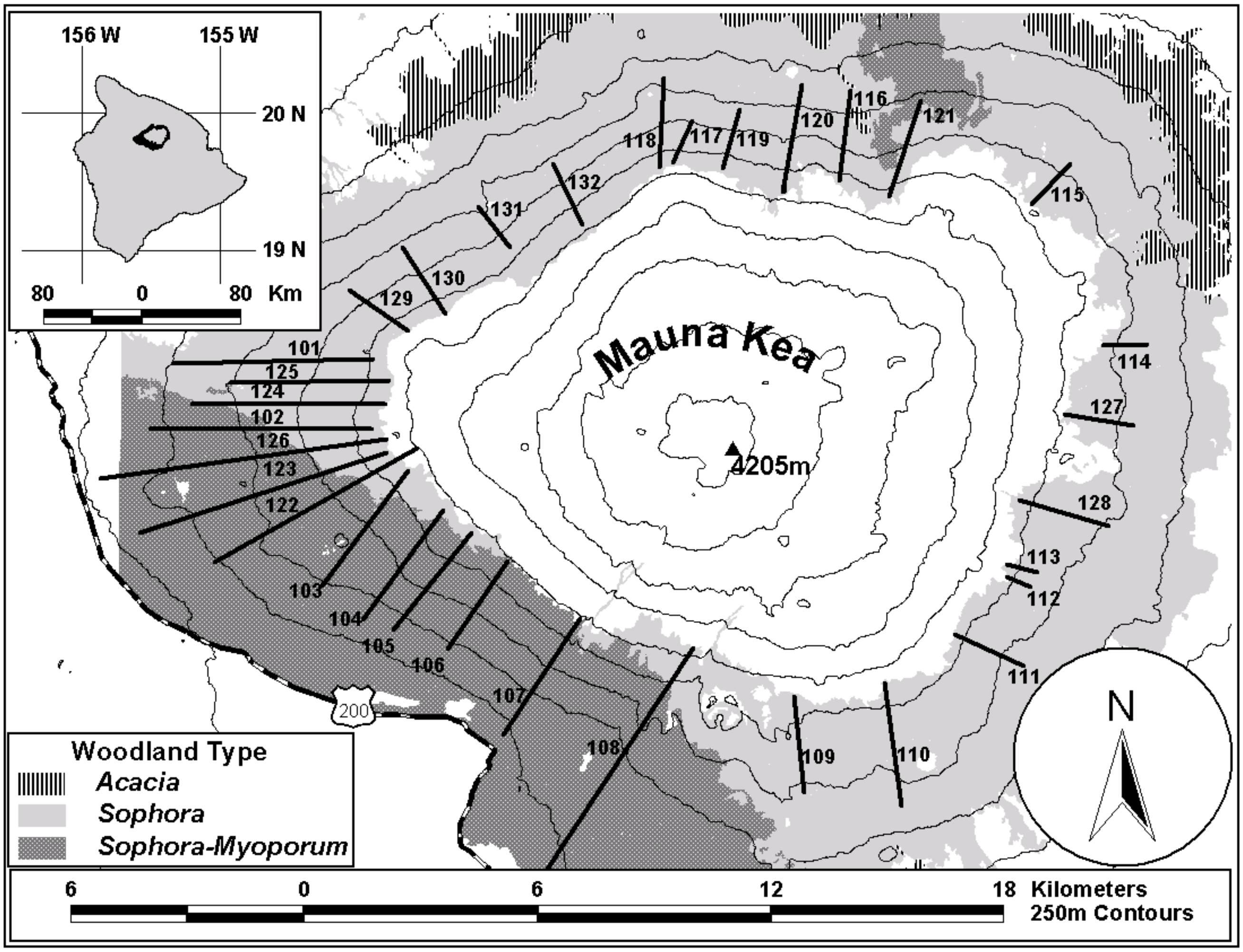

Figure 25.1. Locations of 32 vegetation survey transects on Mauna Kea Hawai'i, February 1999–May 2001.

stratum was recorded only once. We categorized the ground stratum as: bare ground, cinder, dead wood (defined as any woody species that was not rooted to the ground and whose diameter was >5 cm), litter, live vegetation (defined as any vegetation that was rooted and identifiable), rock, and road.

Woody Species Two Meters Tall or Greater

The areas bounded by the point intercept transects formed four 10 x 40 m rectangles or belt transects (Figure 25.2), in which we identified the species present and measured the following variables for woody tree species ≥2 m tall:

1. *Major stem diameter.* All stems ≥5 cm in diameter were measured 10 cm above ground level. The diameter at breast height (DBH) was not recorded because of the branching of māmane stems. Stem diameter was not measured at ground level because surface conditions were usually uneven and rocky and because larger tree trunks bulged at the base.

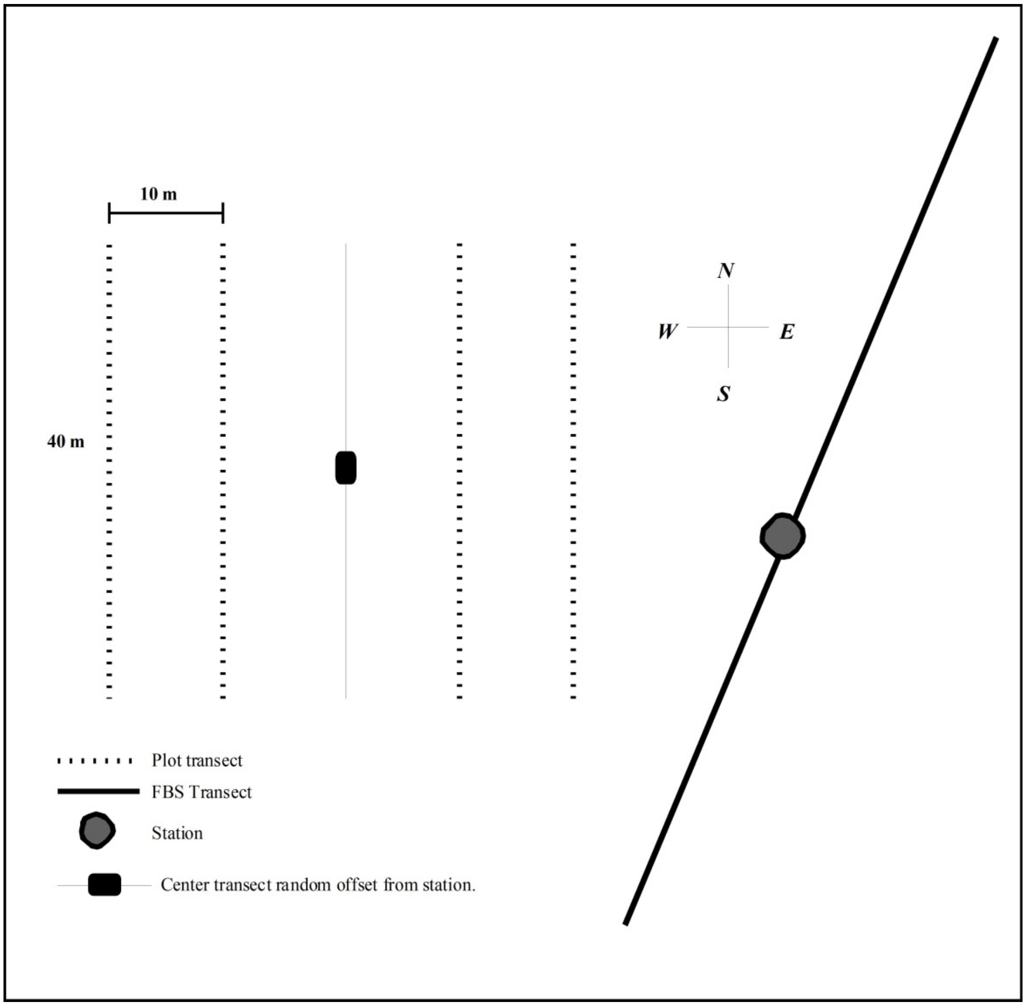

Figure 25.2. Layout of a vegetation survey plot.

2. *Number of minor stems*. Suckers and saplings <5 cm in diameter, >1-m tall, and located within 1 m of the base of the tree or growing from the trunk (>0.5 m above ground) were recorded.
3. *Canopy dimensions*. We measured the following distances to the nearest 0.1 m (Figure 25.3):
   a. Ground (at or extrapolated to the base of the plant) to the lowest foliage
   b. Ground to the highest foliage
   c. Ground to ≥95% of canopy
   d. Ground to ≤95% of canopy
   e. Longest axis of canopy
   f. Longest axis of canopy perpendicular to measurement (e)
4. *Canopy density*. Looking through the center of the crown from all angles, we estimated the percentage of area that was obscured by foliage. The percentage categories recorded were: <5%, 5–49%, 50–95%, >95%.
5. *Canopy vigor*. Tree vigor was assessed according to the prevalence of foliated branches as follows: >95%, 50–95%, 5–49%, and <5% of branches with foliage. The <5%

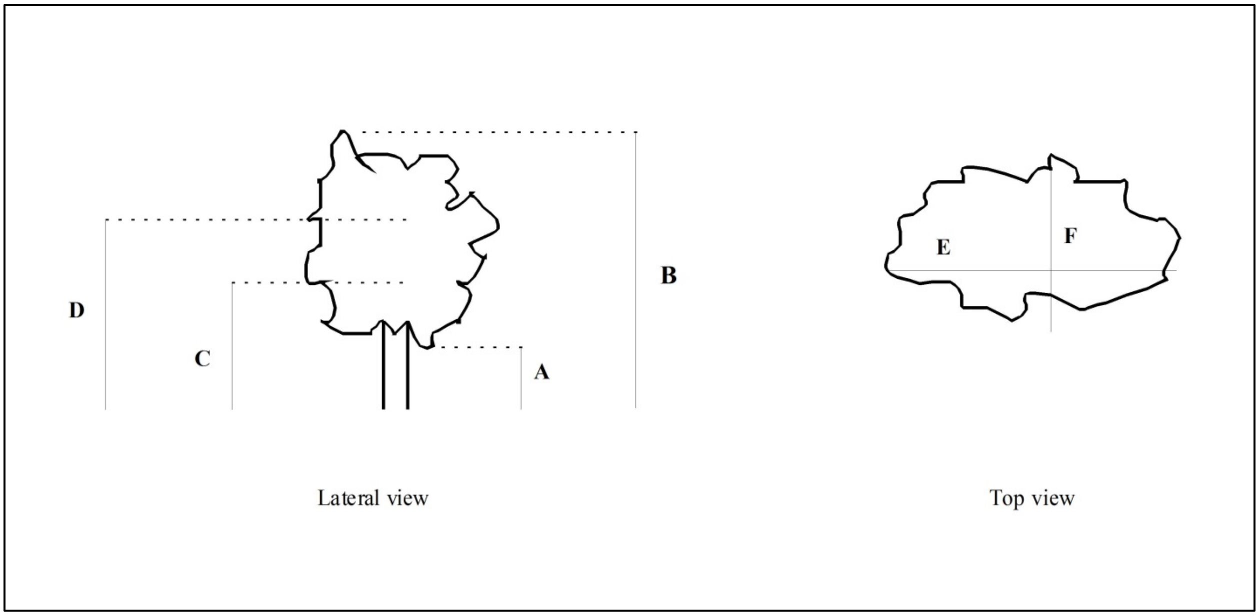

Figure 25.3. Canopy measurements for the vegetation survey of Mauna Kea, Hawai‘i.

category included most branches recently dead and retaining twigs or most branches long dead with few or no twigs present.

6. *Vines*. We recorded the species of vine within the tree's canopy.
7. *Ungulate damage, disturbance, or presence*. Signs of ungulates were recorded in the following categories: none, browse damage, bark stripping, digging within 1 m of the base of the plant, or feces or tracks (identified to genus or species when possible) within 1 m of the base of the plant.
8. *Bird nests*. We recorded species and status (active or inactive) of all nests.

Woody Species Less Than Two Meters Tall

We characterized shrubs and saplings <2 m tall in the same four belt transects utilized for the tree survey. Within each subplot, all woody species were recorded as alive or dead within three height classes (0.2–0.5 m, >0.5–1 m, >1–2 m). Shrubs <0.2 m tall were not recorded because they could be easily overlooked in tall grasses or other dense vegetation. Plants of the same species were considered to be separate individuals if they were separated by at least 0.2 m. Saplings were considered independent of trees when they grew more than 1 m away from a major stem (≥5 cm DBH) of the tree.

Plot Description

We briefly described the sample plot, listed all the species present, and recorded the time to complete our assessment of the plot. We characterized the slope, aspect, and general topography. Human use of the plot was characterized by the amount and type of garbage (e.g., spent shotgun and rifle cartriges, metal cans) found.

Estimating Tree Cover for Palila Critical Habitat

We used the Inverse Distance Weighted model from the Spatial Analyst Extension of ArcView

3.2 (ESRI 1996) to interpolate cover values from each plot to a 300 m^2 cell grid. This model interpolated values across the entire Mauna Kea Forest Reserve.

Results

During the course of the survey we found 180 plant species (Appendix). *Oryzopsis miliacea* represented a new genus of grass in Hawai`i (Dougill and Banko 2002); *Falopia convulvulus* represented a new record for the island of Hawai`i; and three species (*Atriplex canescens*, *Pisum sativum*, and *Pelargonium xhortorum*) were not previously recorded as naturalized species in Hawai`i (for *Atriplex canescens* also see Staples *et al.* 2003). Sixty-nine percent (125/180) of the taxa were alien, 30% (54/180) were indigenous or endemic, and one was possibly indigenous or a Polynesian introduction. Most herbaceous and grass species were alien, whereas most of the trees, shrubs, and ferns were native (Figure 25.4).

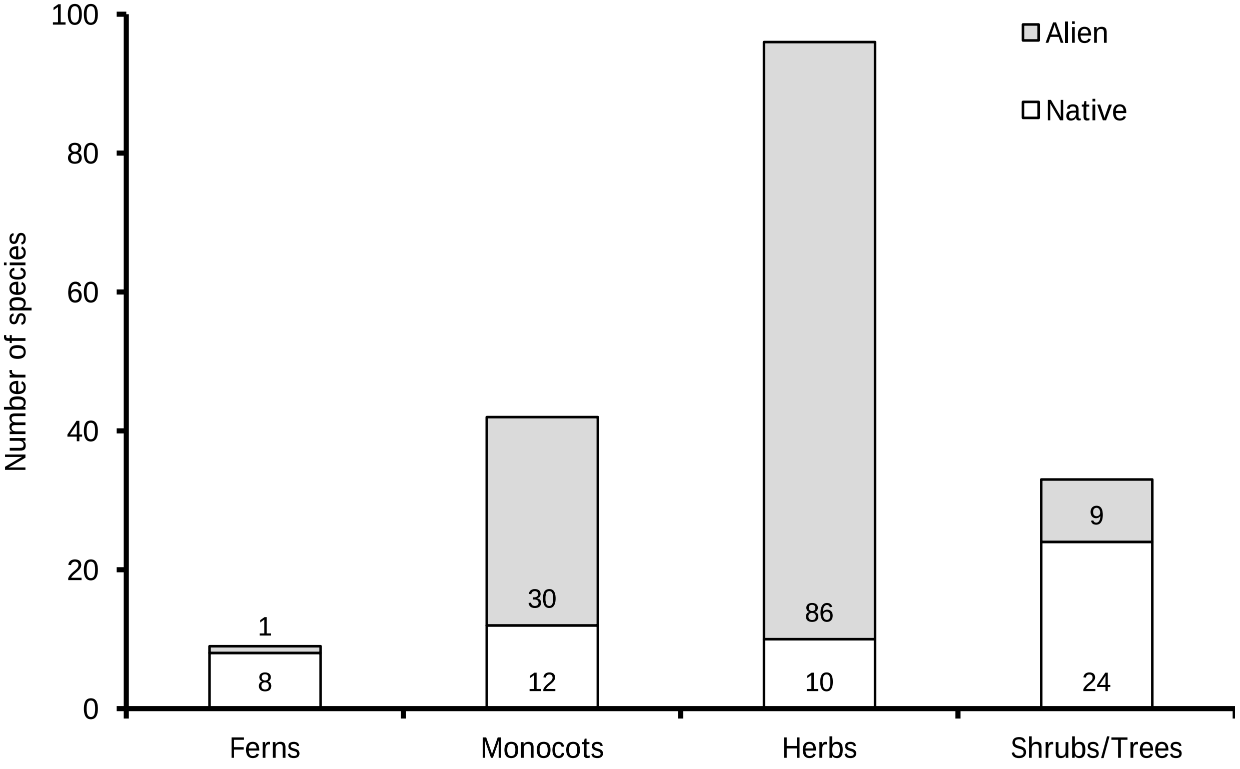

Figure 25.4. Numbers of native and alien plant species in subalpine woodland of Mauna Kea, Hawai`i.

Tree Density and Cover

Trees (≥2 m tall) were widespread in PCH, being found in 434 (86%) of the 504 plots. Tree density per plot averaged 13.5 māmane, 12.4 naio, and 1.8 other species. Tree cover was sparse in PCH as a whole, averaging only 19% overall with māmane composing 7%. Tree cover was greatest on the southwestern slope, especially at mid (24%) and high (25%) elevations, because naio and māmane were relatively abundant (Figure 25.5). At high elevation, tree cover diminished to 13%. Māmane accounted for most of the tree cover elsewhere on Mauna Kea.

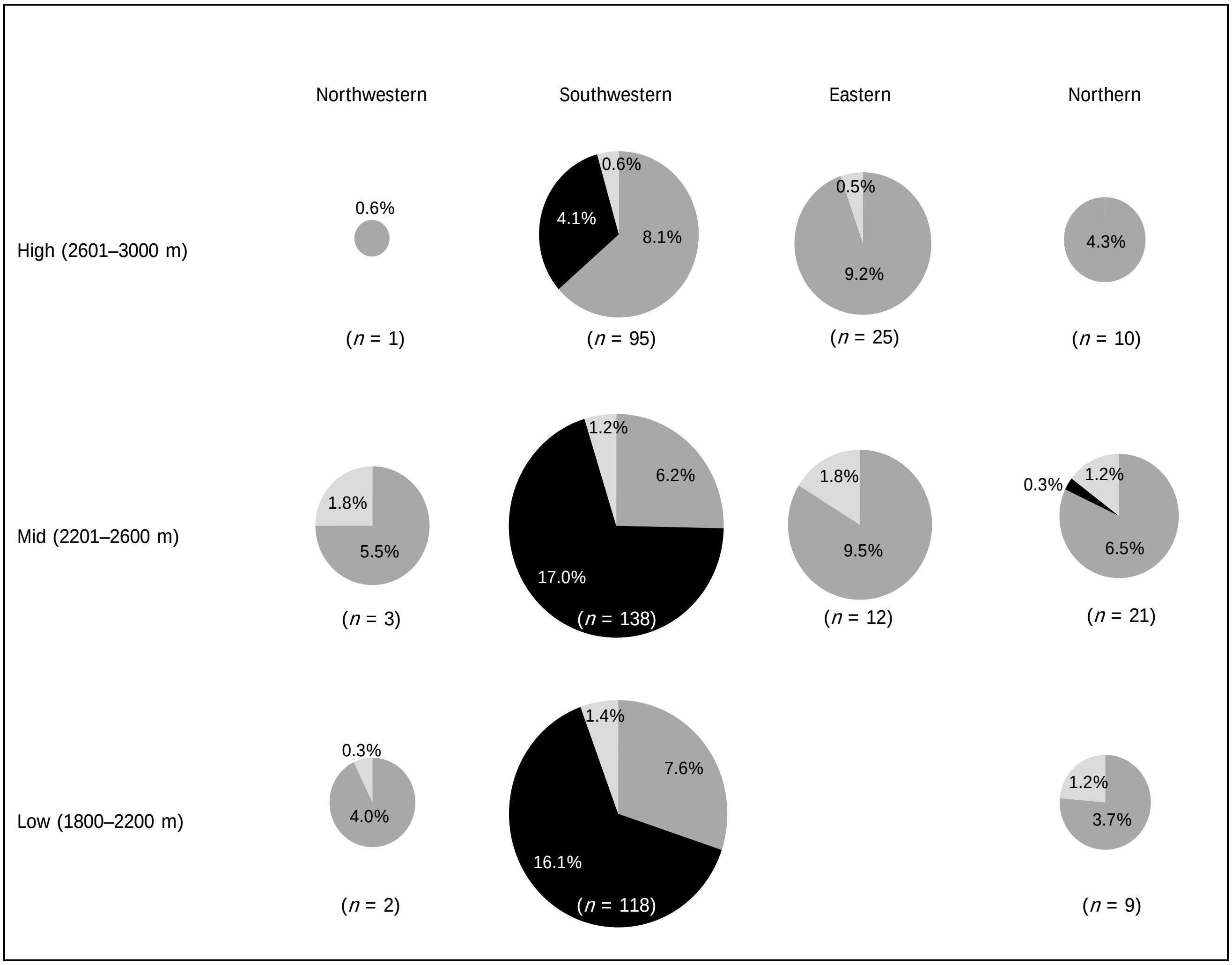

Figure 25.5. Composition of tree canopy cover (māmane = medium grey; naio = black; other species = light grey) on 434 vegetation plots containing trees at low, mid, and high elevations on four slopes of Mauna Kea, Hawai'i, 1999–2001. No plots were surveyed at low elevation on the eastern slope. The size of each pie chart indicates the relative amount of tree cover (0.6–25%; mean = 19%) across that region. The number of vegetation plots containing trees in each region is shown in parentheses.

Māmane canopy cover exceeded 25% in several areas: 1) on the western slope between transects 101 and 102 at mid and high elevations and between transects 102 and 123 at low elevation (Figure 25.1), 2) on the southern slope between transects 108 and 109 close to tree line, 3) on the eastern slope between transects 114 and 115 close to tree line, and 4) on the northern slope along a small portion of transect 116 at mid elevation.

Size Distribution of Māmane and Naio Trees

Māmane tree height averaged 3.7 m (maximum = 11 m), and 61% of māmane trees were <4 m tall. Māmane populations on all four slopes of Mauna Kea were dominated by small trees, although a greater proportion of trees on the eastern slope were >4 m (Figures 25.6 and 25.7).

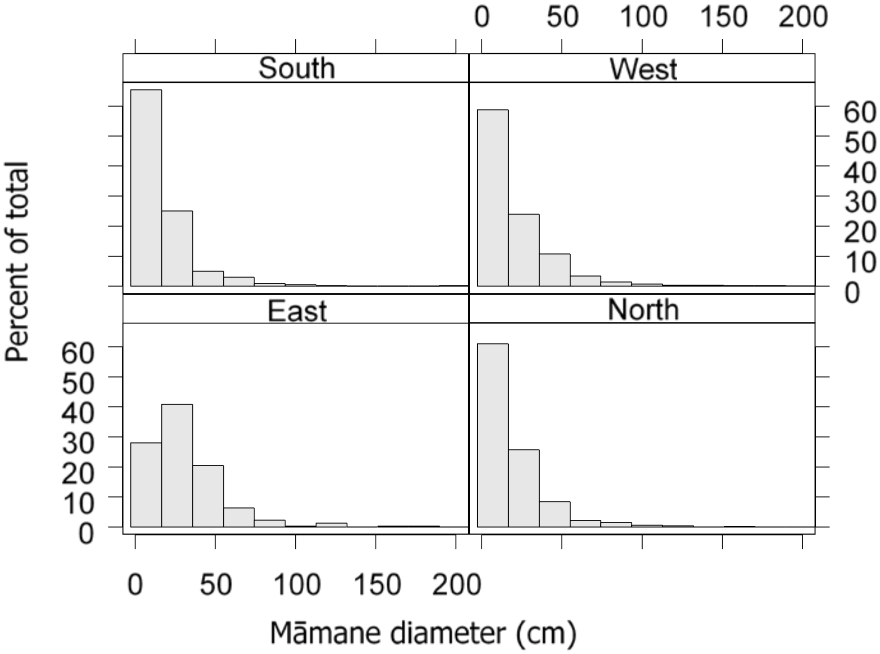

Figure 25.6. Basal diameters of māmane trees from the four slopes of Mauna Kea, Hawai'i, 1999–2001.

A dense, low-stature forest dominated by naio and māmane covered extensive areas of the lower western slope and extended from Pōhakuloa Flats to tree line on the southern flank of Mauna Kea. On the western slope, we found that half (51%) of the māmane population was 2–4 m tall; by contrast, only a third (34%) of naio trees were the same size. On the southern slope, trees tended to be smaller; still, more māmane were 2–4 m tall (79%) compared to naio (67%; Figure 25.8).

Māmane Regeneration

Māmane saplings (<2 m in height) were found in 91% of plots, but only 38% contained densities equivalent to at least one sapling per 100 m^2 (Figure 25.9). Regeneration varied considerably with location; 54% of plots on the eastern slope supported no māmane regeneration, compared to 5% on the western slope (Table 25.1). Overall, māmane saplings were more abundant on the western and northern slopes and at higher elevations (Figure 25.10).

Dead Trees

We found dead and dying māmane trees throughout PCH. Dead or dying trees were most

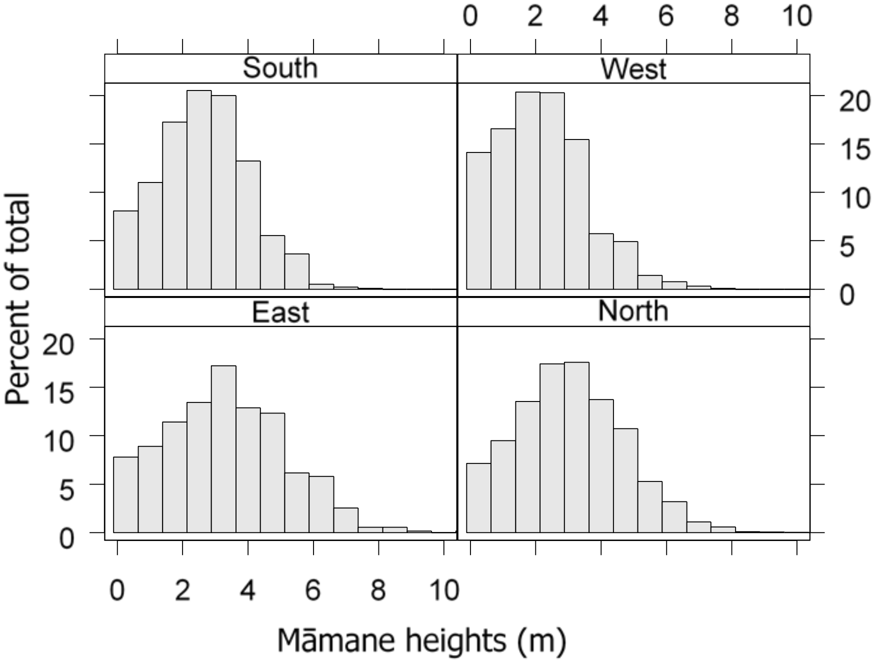

Figure 25.7. Heights of māmane trees from the four slopes of Mauna Kea, Hawai'i, 1999−2001.

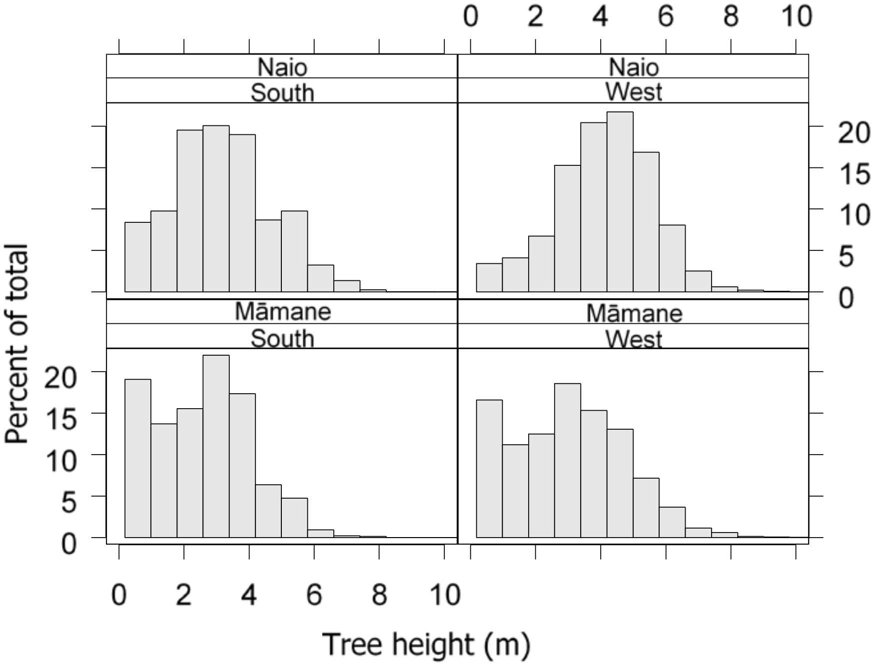

Figure 25.8. Heights of māmane and naio trees in mixed subalpine woodland from two slopes of Mauna Kea, Hawai'i, 1999−2001.

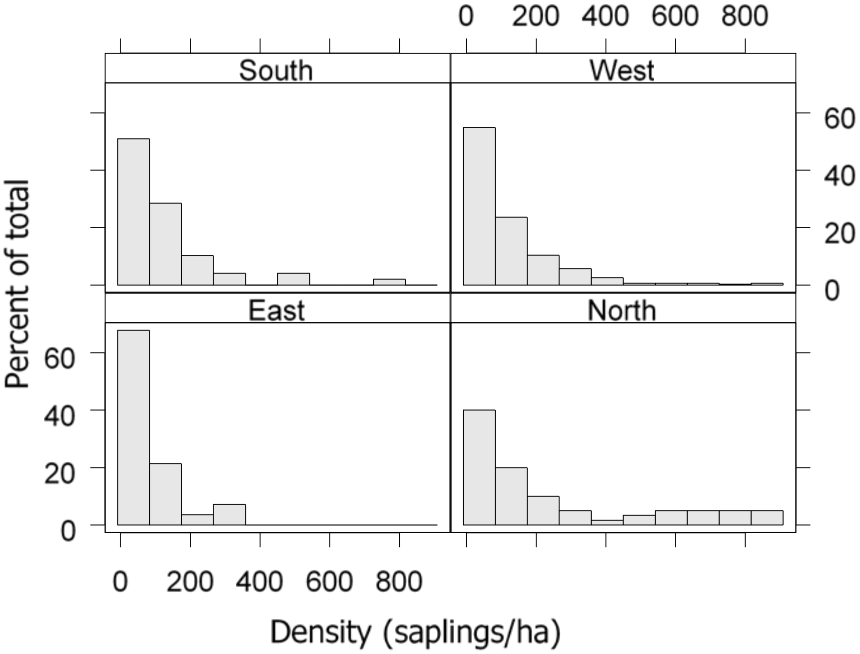

Figure 25.9. Māmane sapling density on the four slopes of Mauna Kea, Hawai'i, 1999−2001.

Table 25.1. Percent of plots lacking māmane saplings on Mauna Kea, Hawai'i, 1999–2001.

Slope	% plots lacking small saplings (0−1 m)	% plots lacking large saplings (1−2 m)	% plots lacking any saplings
Western	14.5	18.9	4.9
Southern	22.2	22.2	17.2
Eastern	46.2	57.7	53.8
Northern	12.5	26.8	7.1

common on the southern and southeastern slopes and in cattle pastures outside PCH on the western slope (Figure 25.11).

Ungulate Damage

Ungulate damage was observed frequently on vegetation plots on the southwestern slope of Mauna Kea where tree cover was greatest. Sheep browsing or sign was detected on more than half of the plots on the southwestern slope but less frequently on the eastern and northern slopes (Figure 25.12). Sheep sign was nearly absent on the northwestern slope where tree cover was low. Cattle sign was detected on plots outside PCH in pasture on the western slope.

Discussion

Over two-thirds of the 180 plant species we identified on the survey were alien, including several species that had not been recorded previously on Hawai'i Island. Although most herbaceous and grass species were alien, most of the trees, shrubs, and ferns were native.

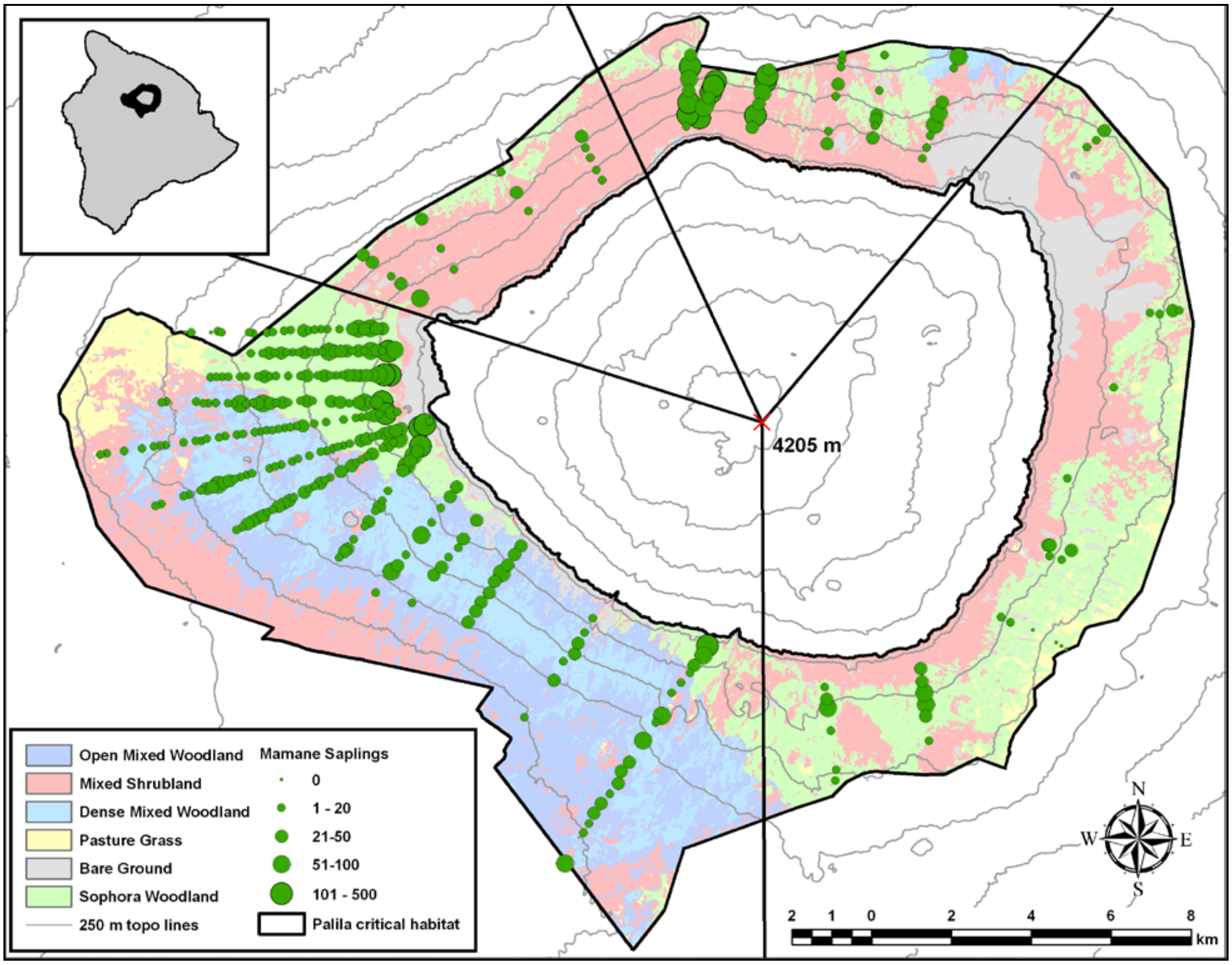

Figure 25.10. Distribution and relative abundance of māmane saplings (<2 m tall) on vegetation plots on four slopes of Mauna Kea, Hawai'i, 1999–2001. Saplings were relatively sparse on the eastern and northwestern slopes and at lower elevations.

Although trees were widely distributed in PCH, tree cover was generally patchy and sparse except on the southwestern slope where naio and māmane were relatively abundant and where palila were concentrated (Banko *et al.* 2013). Māmane was the most broadly distributed tree species, but māmane cover was likely too low to support palila in most areas around Mauna Kea. A small but relatively dense patch of māmane forest on the northern slope was extensively used by palila translocated there during 1997−1998 and 2004−2006 (Banko *et al*. 2009; see Chapter 2: Translocating Wild Palila).

Most māmane trees on Mauna Kea were small, averaging 3.7 m in height. Nearly two-thirds of māmane trees were less than 4 m tall, indicating widespread regeneration within the preceding 25 years, based on the growth models of Scowcroft and Conrad (1988). Although māmane saplings were found in 91% of survey plots, only 38% of plots contained densities equivalent to at least one sapling per 100 m^2. This suggests that habitat restoration is occurring, but not with sufficient speed to prevent steep declines in palila numbers during drought (Banko *et al.* 2013).

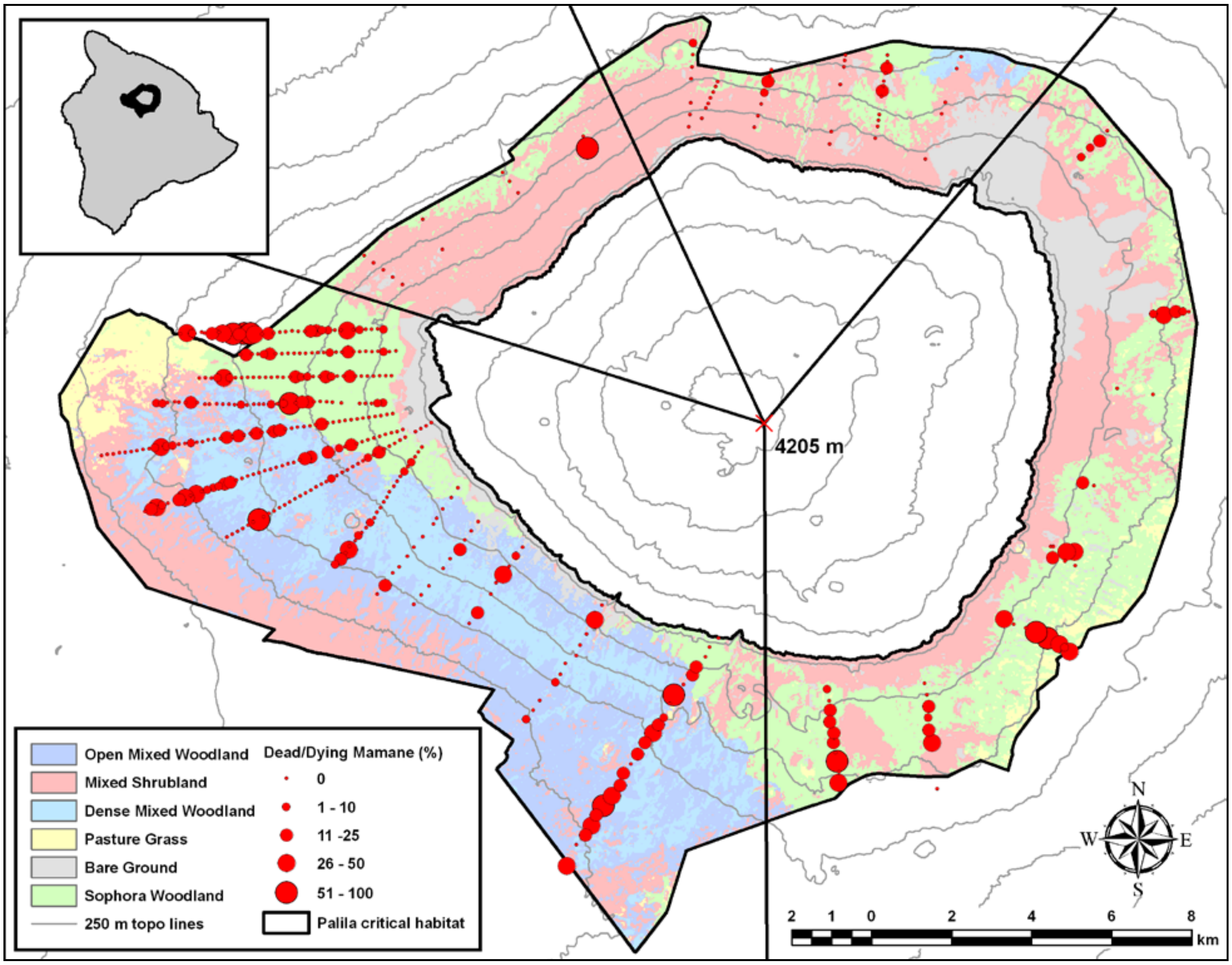

Figure 25.11. Distribution and relative abundance of dead and dying māmane trees (≥2 m tall) on vegetation plots on four slopes of Mauna Kea, Hawaiʽi, 1999–2001. Many dead trees were encountered on the southern and southeastern slopes and in cattle pastures outside Palila Critical Habitat on the western slope.

Palila utilize primarily larger māmane trees (Scott *et al.* 1984, Pletschet and Kelly 1990), presumably because they offer more food resources as well as better concealment from predators and protection from unfavorable environmental conditions. That only 39% of māmane trees are >4 m in height suggests that palila spend most of their time in a limited set of trees across the landscape.

Māmane is preferentially browsed by sheep (Warner 1960, Scowcroft and Giffin 1983), possibly leading to its competitive displacement by naio in the mixed forest (Hess *et al.* 1999). We found evidence of sheep and other ungulates on a majority of plots on the southwestern slope, suggesting that māmane will gain in dominance over naio once browsing is eliminated.

We encountered many dead and dying māmane trees on vegetation plots throughout PCH. We did not identify causes of mortality, but contributing factors may include root rot, browsing, alien weeds, and drought (Banko *et al.* 2013).

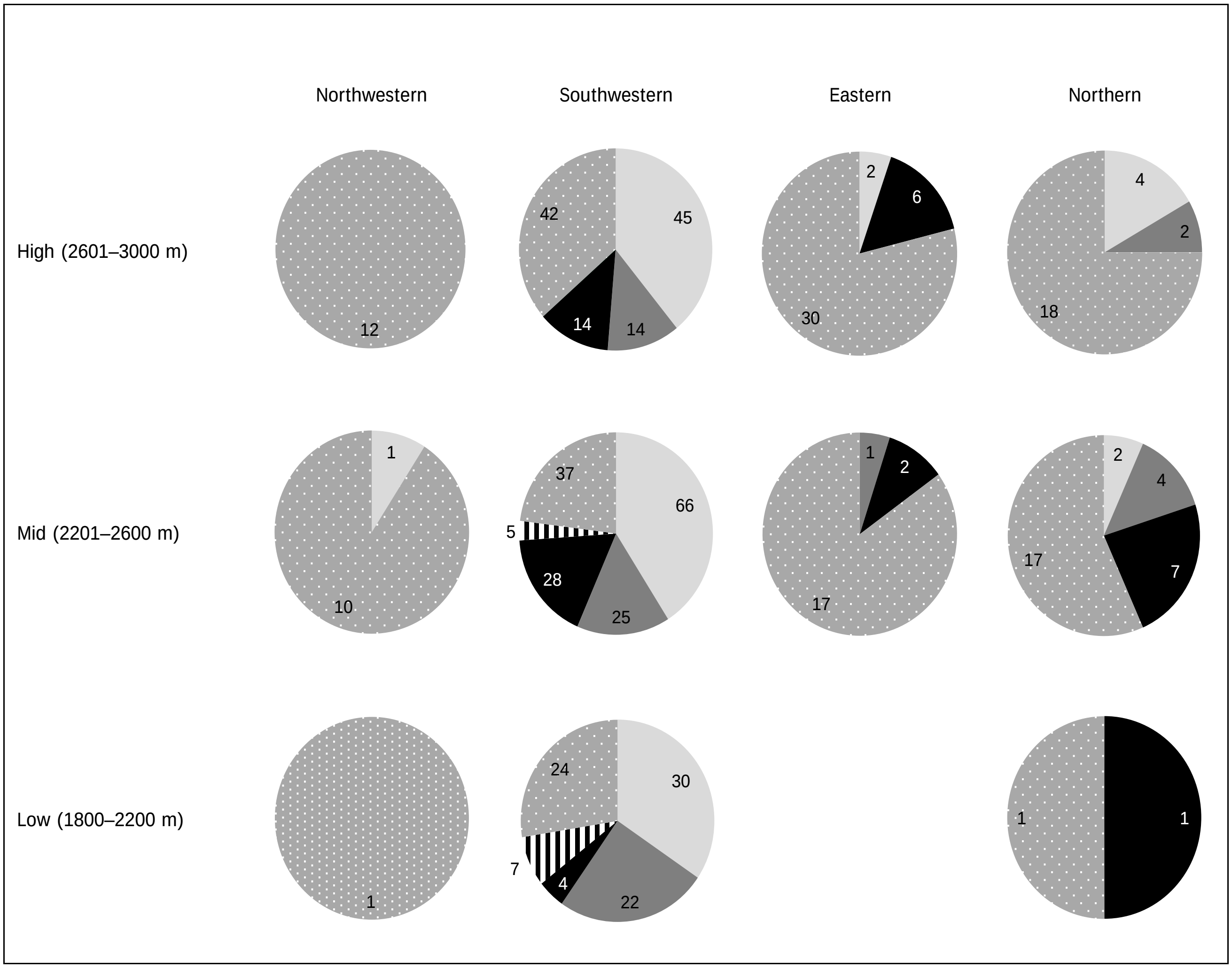

Figure 25.12. Distribution of ungulate damage on 501 vegetation plots at low, mid, and high elevations on four slopes of Mauna Kea, Hawai'i, 1999–2001. No plots were surveyed at low elevation on the eastern slope. Damage categories are illustrated as: no ungulate damage = grey stipple; sheep browse or sign = light grey; pig digging or sign = black; sheep and pig sign = dark grey; cattle browsing or sign = bars. Numbers of vegetation plots affected are shown within each pie chart section.

The woody vegetation of PCH is dominated by a few native species that are critically important to the endangered palila. This māmane woodland is dynamic with widespread regeneration of māmane but also with relatively high levels of mortality. The key to recovering the palila is to ensure that māmane cover increases as rapidly as possible.

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Appendix: Vascular Plant Species

Vascular plant species and subspecies collected in the subalpine forest of Mauna Kea, Hawai'i, November 1998–May 2001. Species are arranged alphabetically by family and genus. Geographic status (Wagner *et al*. 1999; L. Pratt, U.S. Geological Survey, personal communication) and life cycle data for each taxon:

Endemic:	occurring naturally only in the Hawaiian Archipelago
Indigenous:	occurring naturally within the Hawaiian Archipelago but also occurring elsewhere
Indigenous(?):	probably indigenous, but possibly naturalized
Naturalized:	introduced by humans and their activities; established and reproducing
Adventive:	introduced by humans and their activities; established only locally or ephemerally
Perennial:	a plant that lives two or more years and the above-ground parts either die-back once a year (herbaceous perennial) or remain alive for many years (woody perennial)
Annual:	a plant completing its life cycle within one year

Taxon	Geographic status	Life cycle
FERNS		
ASPLENIACEAE		
Asplenium adiantum-nigrum	indigenous	perennial
Asplenium trichomanes densum	indigenous	perennial
DENNSTAEDTIACEAE		
Pteridium aquilinum decompositum	endemic	perennial
DRYOPTERIDACEAE		
Dryopteris wallichiana	indigenous	perennial
Polystichum hillebrandii	endemic	perennial
OPHIOGLOSSACEAE		
Ophioglossum nudicaule	indigenous	perennial
PTERIDACEAE		
Adiantum raddianum	naturalized	perennial
Pellaea ternifolia	indigenous	perennial
Pteris cretica	indigenous	perennial
GRASSES / SEDGES / RUSHES		
CYPERACEAE		
Carex macloviana subfusca	indigenous	perennial
Carex meyenii	indigenous	perennial
Carex wahuensis	endemic	perennial
JUNCACEAE		
Luzula hawaiiensis	endemic	perennial
Juncus tenuis	naturalized	perennial
POACEAE		
Agrostis sandwicensis	endemic	perennial

Taxon	Geographic status	Life cycle
Anthoxanthum odoratum	naturalized	perennial
Arrhenatherum elatius	naturalized	perennial
Avena fatua	naturalized	perennial
Bromus catharticus	naturalized	annual/perennial
Bromus diandrus	naturalized	annual
Bromus hordaceus	naturalized	annual/perennial
Cenchrus clandestinus	naturalized	perennial
Cenchrus setaceus	naturalized	perennial
Chloris radiata	naturalized	perennial
Cynodon dactylon	naturalized	perennial
Dactylis glomerata	naturalized	perennial
Deschampsia nubigena	endemic	perennial
Ehrharta calycina	naturalized	perennial
Ehrharta stipoides	naturalized	perennial
Elymus triticoides	uncertain[1]	perennial
Eragrostis atropioides	endemic	perennial
Eragrostis brownii	naturalized	perennial
Eragrostis leptophylla	endemic	perennial
Festuca bromoides	naturalized	perennial
Festuca rubra	naturalized	perennial
Holcus lanatus	naturalized	perennial
Hordeum murinum leporinum	naturalized	perennial
Lachnagrostis filiformis	indigenous	annual
Lolium perenne	naturalized	perennial
Melinis minutiflora	naturalized	perennial
Oryzopsis miliacea	naturalized	perennial
Panicum pellitum	endemic	annual
Panicum tenuifolium	endemic	perennial
Poa pratensis	naturalized	perennial
Poa annua	naturalized	annual
Melinis repens	naturalized	annual/perennial
Rhytidosperma penicillatum	naturalized	perennial
Sporobolus africanus	naturalized	perennial
Sporobolus indicus	naturalized	perennial
Stipa cernua	naturalized	perennial
Trisetum glomeratum	endemic	perennial
HERBS		
APIACEAE		
Daucus pusillus	naturalized	perennial
Foeniculum vulgare	naturalized	perennial
Petroselinum crispum	naturalized	perennial
Sanicula sandwicensis	endemic	perennial
ASTERACEAE		
Achillea millefolium	naturalized	perennial
Bidens alba	naturalized	annual/perennial
Cirsium vulgare	naturalized	perennial

Taxon	Geographic status	Life cycle
Conyza bonariensis	naturalized	annual
Crepis capillaris	naturalized	annual/perennial
Delairea odorata	naturalized	annual
Euchiton sphaericus	naturalized	annual
Galinsoga parviflora	naturalized	annual
Gamochaeta purpurea	naturalized	perennial
Helichrysum foetidum	naturalized	perennial
Heterotheca grandiflora	naturalized	annual/perennial
Hypochoeris glabra	naturalized	perennial
Hypochoeris radicata	naturalized	perennial
Lactuca spp.	naturalized	perennial
Leucanthemum vulgare	naturalized	perennial
Picris hieracioides	naturalized	perennial
Pseudognapahlium sandwicensium	endemic	perennial
Senecio madagascariensis	naturalized	perennial
Senecio sylvaticus	naturalized	annual
Senecio vulgaris	naturalized	annual
Sigesbeckia orientalis	naturalized	annual
Sonchus asper	naturalized	annual
Sonchus oleraceus	naturalized	annual
Tagetes minuta	naturalized	annual
Taraxacum officinale	naturalized	perennial
Tragopogon dubius	naturalized	perennial
Verbesina encelioides	naturalized	annual
BRASSICACEAE		
Brassica nigra	naturalized	annual
Capsella bursa-pastoris	naturalized	annual
Lepidium africanum	naturalized	perennial
Lepidium bonariense	naturalized	perennial
Lepidium virginicum	naturalized	perennial
Raphanus sativus	naturalized	annual
Sisymbrium irio	naturalized	annual
Sisymbrium officinale	naturalized	annual
CAMPANULACEAE		
Wahlenbergia gracilis	naturalized	perennial
CARYOPHYLLACEAE		
Arenaria serpyllifolia	naturalized	annual
Cerastium fontanum triviale	naturalized	perennial
Dianthus armeria	naturalized	annual/perennial
Polycarpon tetraphyllum	naturalized	annual
Stellaria media	naturalized	annual/perennial
CHENOPODIACEAE		
Atriplex semibaccata	naturalized	perennial

Taxon	Geographic status	Life cycle
Chenopodium murale	naturalized	annual
Dysphania ambrosioides	naturalized	annual/perennial
Salsola tragus	naturalized	annual
CUCURBITACEAE		
Sicyos anunu	endemic	annual
EUPHORBIACEAE		
Euphorbia peplus	naturalized	annual
FABACEAE		
Medicago lupulina	naturalized	annual/perennial
Medicago polymorpha	naturalized	annual/perennial
Medicago sativa	naturalized	annual/perennial
Melilotus alba	naturalized	perennial
Pisum sativum	naturalized	annual
Trifolium arvense	naturalized	annual
Trifolium dubium	naturalized	annual
Trifolium pratense	naturalized	perennial
Trifolium repens	naturalized	perennial
Vicia sativa nigra	naturalized	annual
Vicia villosa	naturalized	perennial
GENTIANACEAE		
Centaurium erythraea	naturalized	perennial
GERANIACEAE		
Erodium cicutarium	naturalized	annual
Geranium homeanum	naturalized	perennial
Pelargonium xhortorum	adventive	perennial
IRIDACEAE		
Sisyrinchium acre	endemic	annual
LAMIACEAE		
Marrubium vulgare	naturalized	perennial
Stenogyne microphylla	endemic	perennial
Stenogyne rugosa	endemic	perennial
LINACEAE		
Linum bienne	naturalized	annual/perennial
MALVACEAE		
Malva parviflora	naturalized	perennial
Modiola caroliniana	naturalized	perennial
ONAGRACEAE		

Taxon	Geographic status	Life cycle
Epilobium billardierianum	naturalized	perennial
Oenothera stricta	naturalized	annual
OXALIDACEAE		
Oxalis corniculata	indigenous(?)[2]	perennial
PAPAVERACEAE		
Argemone glauca	endemic	perennial
Eschscholzia californica	naturalized	annual/perennial
PLANTAGINACEAE		
Plantago lanceolata	naturalized	perennial
POLYGONACEAE		
Emex spinosa	naturalized	annual/perennial
Falopia convulvulus	naturalized	annual
Rumex acetosella	naturalized	perennial
Rumex obtusifolius	naturalized	perennial
PRIMULACEAE		
Anagallis arvensis	naturalized	annual/perennial
RANUNCULACEAE		
Ranunculus hawaiensis	endemic	perennial
RUBIACEAE		
Galium divaricatum	naturalized	annual
Sherardia arvensis	naturalized	annual
SCROPHULARIACEAE		
Verbascum thapsus	naturalized	perennial
Verbascum virgatum	naturalized	perennial
Veronica serpyllifolia	naturalized	perennial
SOLANACEAE		
Datura stramonium	naturalized	annual
Solanum americanum	indigenous?	annual/perennial
URTICACEAE		
Hesperocnide sandwicensis	endemic	annual
Urtica urens	naturalized	annual
VERBENACEAE		
Verbena litoralis	naturalized	perennial
Verbena rigida	naturalized	perennial
SHRUBS / TREES		

Taxon	Geographic status	Life cycle
ASTERACEAE		
Argyroxiphium sandwicense sandwicense	endemic	perennial
Bidens menziesii filiformis	endemic	perennial
Dubautia arborea	endemic	perennial
Dubautia ciliolata	endemic	perennial
Dubautia linearis	endemic	perennial
Pluchea carolinensis	naturalized	perennial
Tetramolopium humile	endemic	perennial
CACTACEAE		
Opuntia ficus-indica	naturalized	perennial
CARYOPHYLLACEAE		
Silene gallica	naturalized	perennial
Silene struthioloides	endemic	perennial
CHENOPODIACEAE		
Atriplex canescens	naturalized	perennial
Chenopodium oahuense	endemic	perennial
EPACRIDACEAE		
Leptecophylla (Styphelia) tameiameiae	indigenous	perennial
ERICACEAE		
Vaccinium reticulatum	endemic	perennial
EUPHORBIACEAE		
Euphorbia olowaluana	endemic	perennial
FABACEAE		
Acacia koa	endemic	perennial
Sophora chrysophylla	endemic	perennial
Ulex europaeus	naturalized	perennial
GERANIACEAE		
Geranium cuneatum	endemic	perennial
LYTHRACEAE		
Lythrum maritimum	naturalized	perennial
MALVACEAE		
Sida fallax	indigenous	perennial
MYOPORACEAE		
Myoporum sandwicense	indigenous	perennial

Taxon	Geographic status	Life cycle
MYRTACEAE		
Syzygium cumini	naturalized	perennial
POLYGONACEAE		
Rumex giganteus	endemic	perennial
ROSACEAE		
Osteomeles anthyllidifolia	indigenous	perennial
Rubus hawaiensis	endemic	perennial
RUBIACEAE		
Coprosma ernodeoides	endemic	perennial
Coprosma montana	endemic	perennial
SANTALACEAE		
Santalum paniculatum	endemic	perennial
SAPINDACEAE		
Dodonaea viscosa	indigenous	perennial
SOLANACEAE		
Physalis peruviana	naturalized	perennial
Solanum pseudocapsicum	naturalized	perennial
THYMELAECEAE		
Wikstroemia phillyreifolia	endemic	perennial

[1] Status listed as uncertain, but collected at Humu‘ula on Mauna Kea in 1936 (Wagner *et al.* 1999), suggesting that it has been reproducing for decades, if only locally.

[2] Status listed as possibly indigenous or Polynesian introduction by Wagner *et al.* (1999).

Wagner, W. L., D. R. Herbst, and S. H. Sohmer. 1999. Revised edition. Manual of the flowering plants of Hawai‘i. Bishop Museum Special Publication 97. University of Hawai‘i Press and Bishop Museum Press, Honolulu, HI.

26 VEGETATION SURVEYS ON MITIGATION PARCELS

Chris Farmer, Jennifer Higashino, Kalei Rapozo, Paul C. Banko

Introduction

Palila (*Loxioides bailleui*) are in danger of extinction largely because they are concentrated on the western slope of Mauna Kea (Jacobi *et al*. 1996, Banko *et al*. 1998, Gray *et al*. 1999). This species relies upon high densities of māmane (*Sophora chrysophylla*) trees for food and nesting, and the western slope of Mauna Kea has some of the largest concentrations of this tree species remaining. Palila also exhibit strong site tenacity, so they tend to stay in their small breeding area on the western slope (Scott *et al*. 1981, Fancy *et al*. 1993; but see Chapter 12: Habitat Use, Home Range, and Movements for contrary evidence).

The natural vegetation structure of Mauna Kea has been substantially degraded during the last 200 years, primarily from the impacts of introduced feral ungulates (Hartt and Neal 1940, Warner 1960, Scowcroft and Sakai 1983) but also from the invasion of a variety of pests and weeds (Banko *et al*. 2002). This has opened the habitat to further degradation from invasive weeds, such as non-native grasses, that in turn increase the fire potential of the region. These same processes and resultant habitat degradation have occurred throughout the entire historic range of palila (Hartt and Neal 1940, Warner 1960, Scowcroft and Sakai 1983, Banko *et al.* 2009).

Eight sites were evaluated as potential palila habitat based on forest composition, structure, recruitment, and food resources (see Chapter 1: Evaluating Sites for Reintroduction). This research identified the northern slope of Mauna Kea as providing the balance of assets to liabilities most similar to the western slope. In addition to the Mauna Kea State Forest Reserve area itself, there were approximately 1,900 ha of state pasture lands north of the forest reserve available for native forest restoration (Figure 26.1). This combination of factors made the northern slope the most suitable site to test different translocation methods (see Chapter 2: Translocating Wild Palila).

State lands at Puʽu Mali and Kaʽohe (Figure 26.1) were protected by a conservation easement as partial mitigation for realigning Saddle Road through Palila Critical Habitat and with the primary goal of promoting the recovery of palila habitat (U.S. Fish and Wildlife Service 1998, Federal Highway Administration 1999). They are being added to the Mauna Kea Forest Reserve, and the process may be completed by the end of 2013.

The Puʽu Mali mitigation lands contain a valuable remnant of montane and subalpine dry forests. The area extends from approximately 1,576–2,364 m elevation. It includes an ʽaʽā flow with a relatively intact māmane forest in the eastern third; the other two-thirds being pasturelands that have scattered remnants of native vegetation. The lower reaches were most likely a koa (*Acacia koa*)-māmane forest community type, but they have largely been converted to pasture (Figure 26.2; Jacobi 1989, 1990; Wagner *et al*. 1999). The vegetation remaining on the parcel suggested that in its undisturbed state the region was dominated by koa in the lower sections, with māmane and ʽakoko (*Euphorbia olowaluana*) in the upper areas and on the lava flow. Some plant diversity remains on the ʽaʽā flow with other canopy species including naʽenaʽe (*Dubautia arborea*), pilo (*Coprosma montana*), ʽiliahi (*Santalum paniculatum*), and naio (*Myoporum sandwicense*). The ʽaʽā lava flow on the eastern side of the mitigation parcel maintains a māmane-dominated forest, with a large population of ʻakoko.

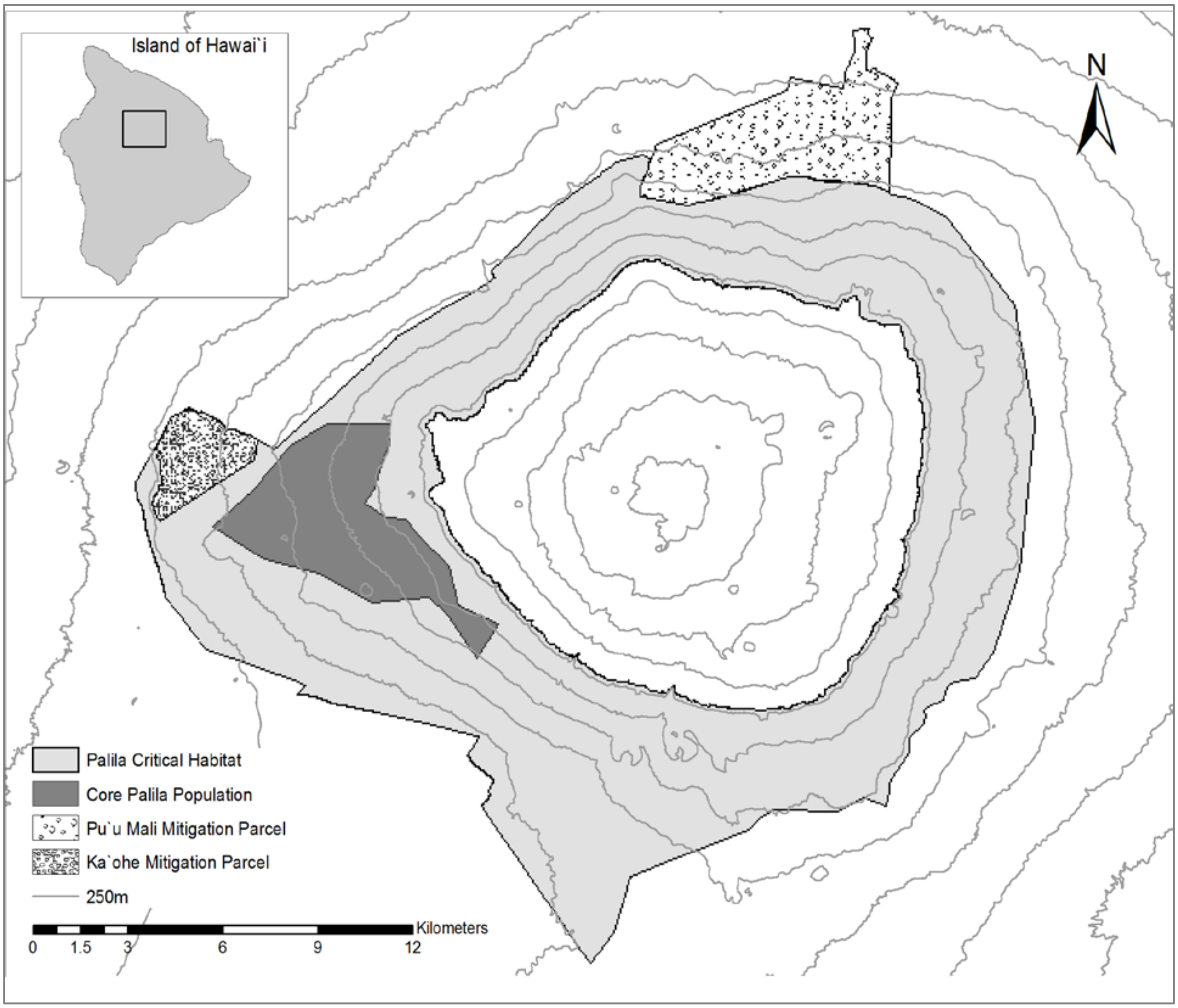

Figure 26.1. Location of Saddle Road mitigation lands and important areas for palila on Mauna Kea, Hawaiʻi.

The Kaʻohe mitigation site is located southwest of Puʻu Laʻau, between 1,770 and 2,150 m elevation. It encompasses approximately 567 ha. The entirety of this parcel is designated critical habitat for palila and is near the core palila habitat (Figures 26.1 and 34.3). Historically, this area was forested with māmane, naio, ʻakoko, ʻiliahi, and other native species. The parcel still maintains some remnants of this forest, although it has been degraded by ungulates and weeds and portions have been completely converted to pasture. The parcel's close proximity to the core palila habitat makes it an important option for future restoration and management.

Construction of the mitigation boundary fences at Kaʻohe and Puʻu Mali were completed in 2006. However, the Puʻu Mali fence was seriously breached in a storm that year and was not fully repaired until 2007. Cattle (*Bos taurus*) were still observed within the boundaries of each parcel until late 2010. Hybrids of wild mouflon sheep (*Ovis gmelini musimon*) and feral sheep (*O. aries*) were removed from Kaʻohe in 2006; the majority were removed from Puʻu Mali by

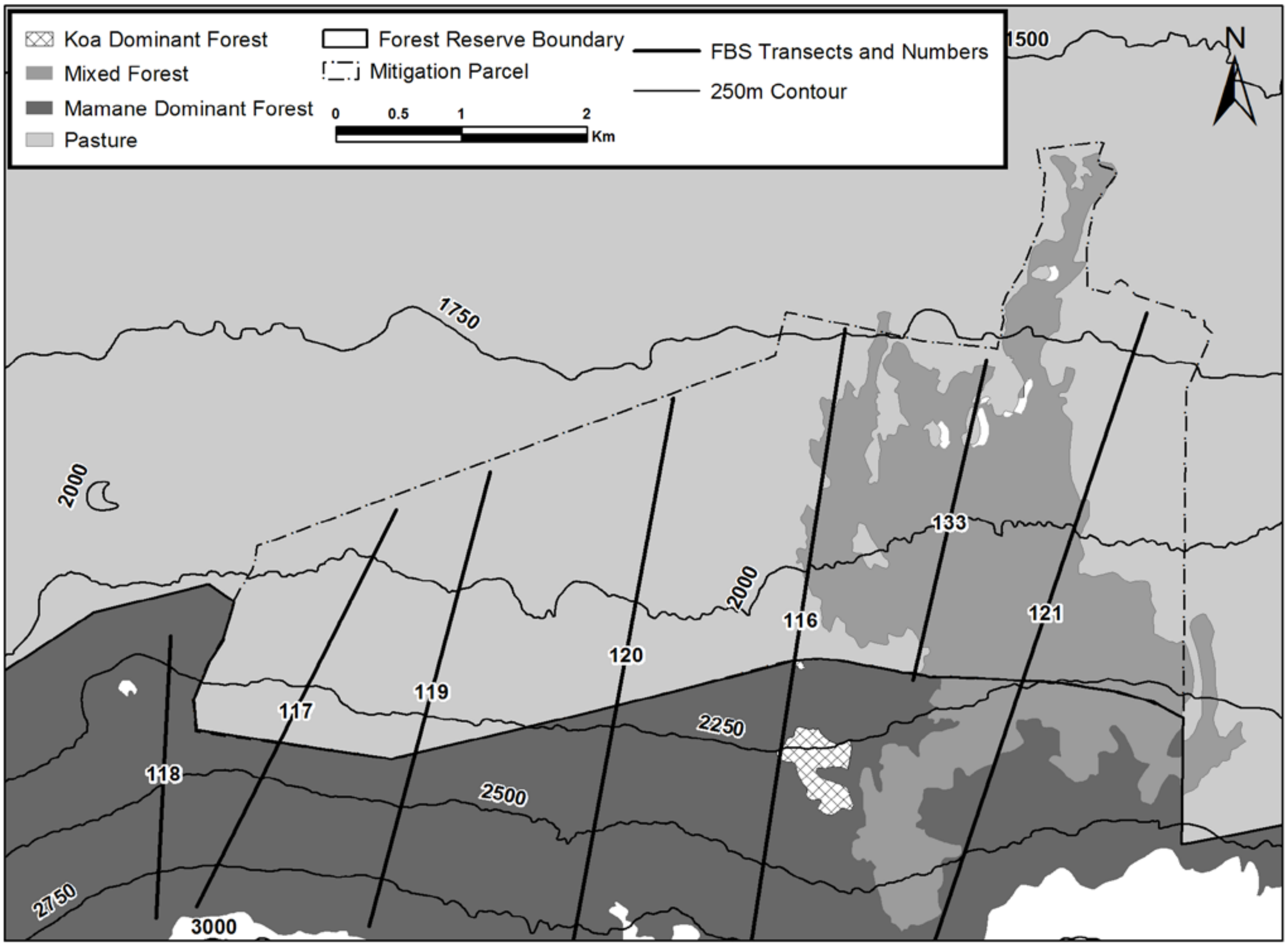

Figure 26.2. Habitat types and survey transects in the Puʻu Mali mitigation parcel on northern Mauna Kea, Hawaiʻi.

2012, although a few stragglers remained as of 2013. Feral pigs (*Sus scrofa*) continued to be found in both parcels through 2013.

To facilitate habitat restoration planning on the mitigation lands, we conducted baseline vegetation surveys at Kaʻohe and Puʻu Mali.

Methods

We extended existing Hawaiʻi Forest Bird Transects (HFBS) on Mauna Kea through the entire Puʻu Mali (Figure 26.2) and Kaʻohe parcels (Figure 26.3). In 2004, we completed baseline vegetation surveys on Transects 121 and 133 in the Puʻu Mali parcel, which were primarily within the ʻaʻā flow. This eastern section contains the majority of the remaining native forest on the parcel, and the relative abundance and diversity of native species there increases its value for restoration. In 2005, we completed surveys of all transects in Puʻu Mali and Kaʻohe. Field assistance for vegetation surveys and other field assessments included staff from: Natural Resources Conservation Service, Pōhakuloa Training Area, Hawaiʻi Division of Forestry and

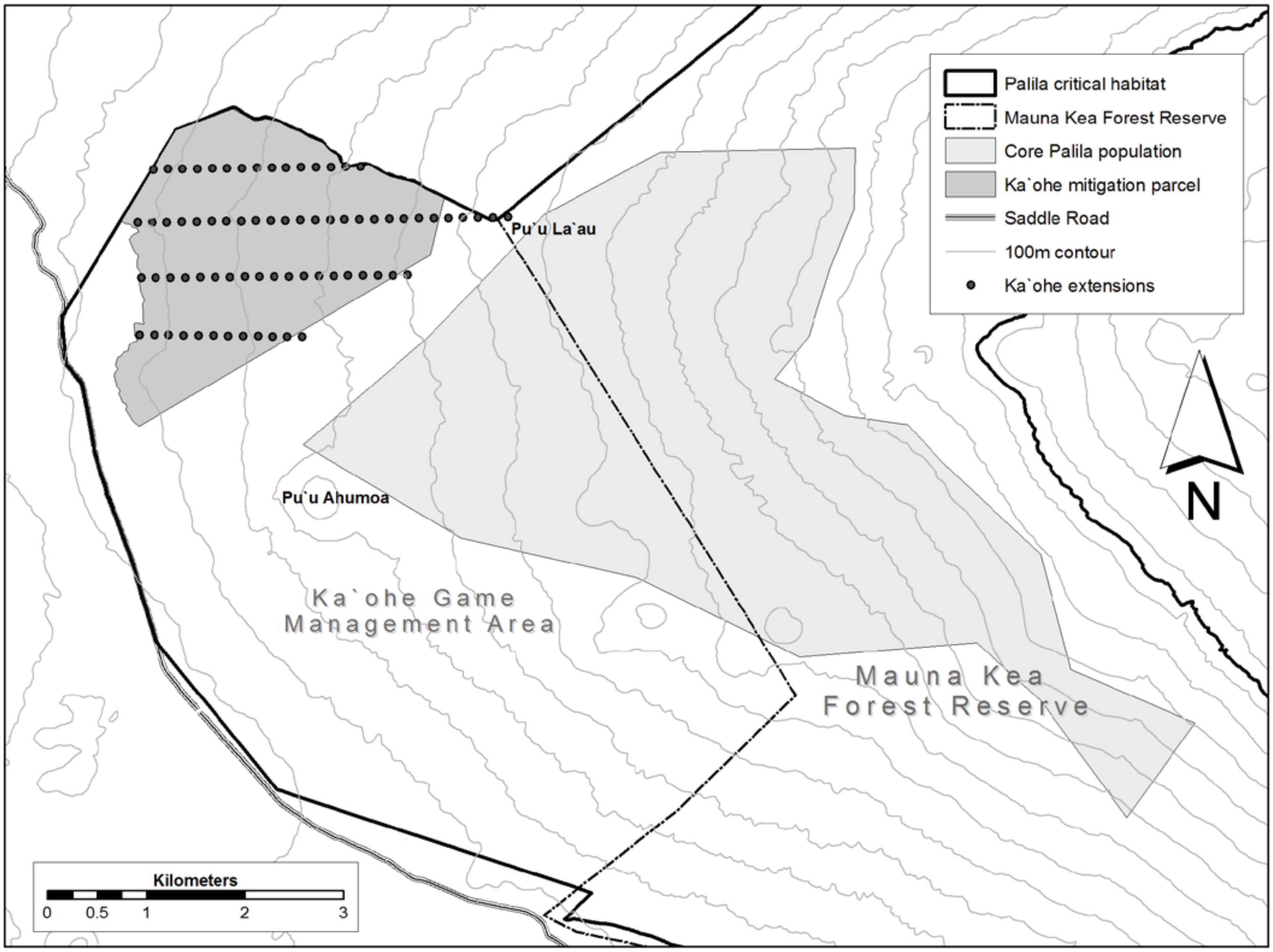

Figure 26.3. Survey sites on the Kaʽohe mitigation parcel with respect to the proximity of core palila habitat on the western slope of Mauna Kea, Hawaiʽi.

Wildlife, West Hawaiʽi Wildfire Management Organization, the National Park Service, as well as teachers from several local high schools.

Our baseline vegetation surveys included sampling various strata of vegetation, photo points, plot descriptions, and assessments of ungulate damage. We established vegetative sampling stations at 150-m intervals along each transect. The actual sampling plot was offset 10 m to the east of each transect to avoid the disturbance due to foot traffic along the transect. Plots were 20 x 20 m with the sides oriented along the cardinal directions. Stations were marked and logged on GPS. We took digital photos of each plot from the southwestern corner, although alternate vantage points were used when necessary. Four survey techniques were conducted within the study plot:

Pole Intercept

We used the pole-intercept technique to assess vegetation composition and structure. We established two 20-m transects on the eastern and western sides of the plot. Vegetation was sampled at 1-m intervals along each transect (21 points per transect, 42 points per plot). At each sample point, we placed a vertical 2-m pole, and recorded where vegetation touched the pole within three separate layers (0–0.5 m, 0.5–1 m, 1–2 m). We estimated where vegetation would touch the pole in the fourth layer (>2 m).

Woody Species Two Meters and Taller

Plots were divided into four 10 x 10 m sub-plots to make counting the trees and shrubs more manageable. These were labeled A, B, C, and D. We recorded the major stem diameter, number of minor stems, canopy density, canopy vigor, and ungulate damage for all woody species ≥2 m in each of the sub-plots.

Woody Species Less Than Two Meters Tall

We characterized shrubs and saplings <2 m tall in the same four sub-plots used for the tree sampling. Within each sub-plot, all woody species were recorded as alive or dead within three height classes (0.2–0.5 m, 0.5–1 m, and 1–2 m). We did not record shrubs <0.2 m in height because some could have been overlooked, reducing the accuracy of our surveys.

Plot Description

We briefly described the general features of the sample plot and listed all the species present. We characterized the slope, aspect, and general topography. In addition, ungulate sign and browsing damage were recorded.

Results

We encountered five tree species within the Puʽu Mali parcel (Figure 26.4). All five species were recorded on the ʽaʽā flow (transects 121, 133, 116), compared to two species on the deep ash substrates, which were dominated by pasture grasses (Figure 26.4). Tree numbers tended to be greater along the ʽaʽā transects, especially 121. We found a more depauperate community in Kaʽohe, with only two tree species (Figure 26.5).

We discovered a new location of *Bidens campylotheca campylotheca* near Puʽu Mali cabin. Five individual plants were found on 15 June 2005. This native shrub is listed as a “species of concern” by the U.S. Fish and Wildlife Service.

Cattle were observed throughout both mitigation parcels during the surveys. Hybrid sheep were seen in the Puʽu Mali parcel during surveys in both years, and sheep and pig sign was frequently recorded on the higher-elevation stations along the forest reserve boundary (Figure 26.2). Sheep browsing damage was observed frequently, particularly near the forest reserve boundary on the Puʽu Mali lava flow. Six goats (*Capra hircus*), including one kid, were observed in the forest reserve above Puʽu Mali on 15 June 2005. A large herd of goats (approximately 10–15) were also observed on the Mauna Kea side of Saddle Road in the area of Puʽu Loa, 20–21 June 2005.

We encountered fireweed (*Senecio madagascarensis*) frequently around the Puʽu Mali mitigation parcel, especially along roads. We also detected incipient populations of several other weed species of concern: two locations of fountain grass (*Cenchrus setaceus*), several locations of cape ivy (*Delairea odorata*), and scattered banana poka (*Passiflora tarminiana*) populations. Although we found few individuals of each species, we took action to prevent their spread. Both populations of fountain grass were flowering and setting seed; we uprooted all plants, bagged them, and disposed of them. Locations were mapped with GPS and were monitored on a

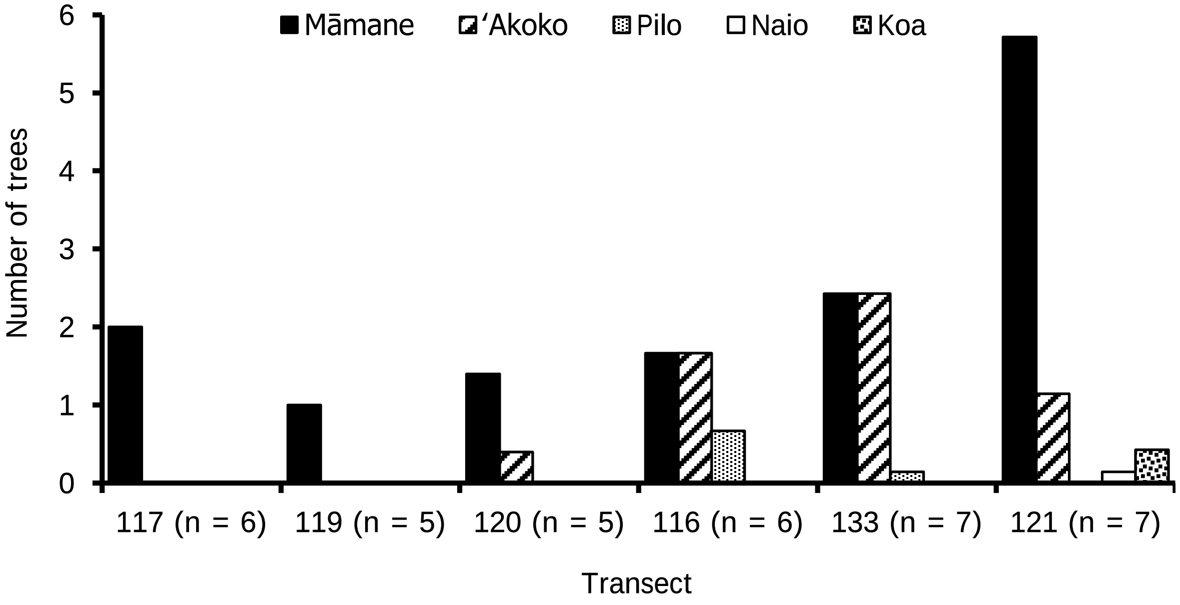

Figure 26.4. Mean number of live trees detected per plot along Forest Bird Survey transects (*n* = number of plots per transect) within the Puʻu Mali mitigation parcel, Mauna Kea, Hawaiʻi, during 2004–2005.

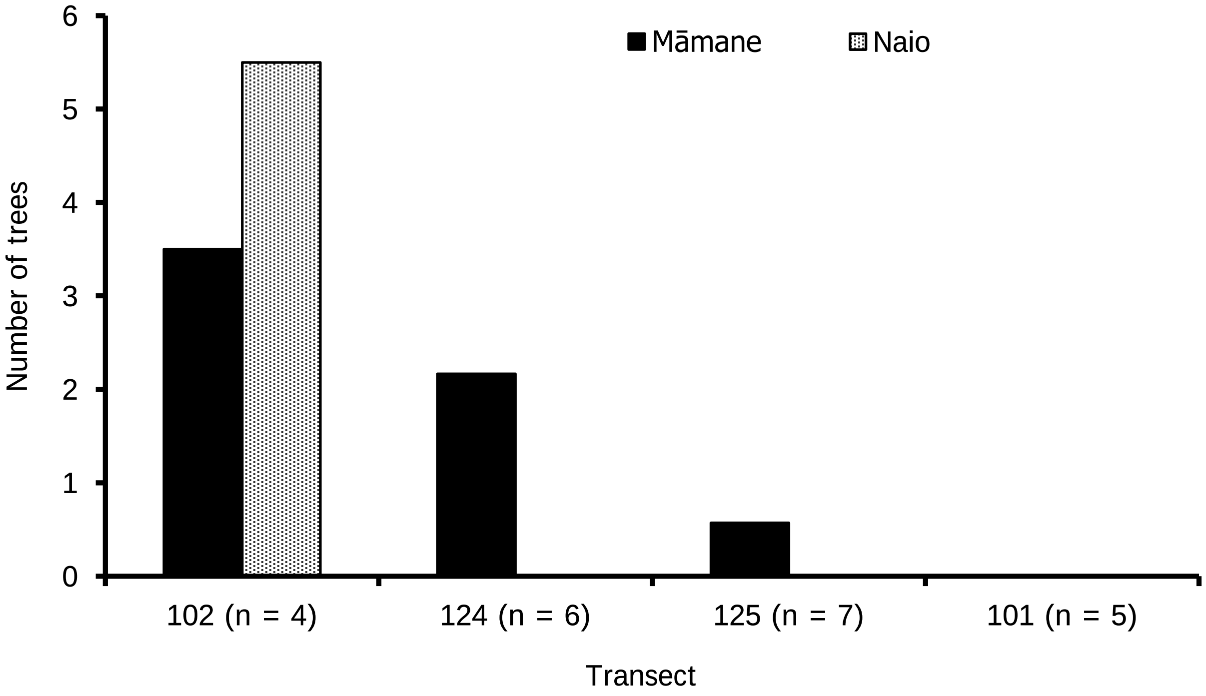

Figure 26.5. Mean number of live trees detected per plot along Forest Bird Survey transects (*n* = number of plots per transect) within the Kaʻohe mitigation parcel, Mauna Kea, Hawaiʻi, in 2005.

quarterly basis to prevent the species from re-establishing. Cape ivy was found near transect 121 and required the use of herbicide after cattle were removed from the area.

We had observed banana poka in the region previously, both in the southeastern portion of the mitigation site and directly above in Mauna Kea Forest Reserve. The plants we found were large and fruiting. We marked the site with GPS, cut the plants at their base, and disposed of all fruit off-site.

At Ka`ohe, we found cape ivy in six plots and frequently found it outside our study plots. Fountain grass was not observed within the Ka`ohe parcel during our surveys. Fireweed was widespread, and we encountered it in all 22 of our plots in Ka'ohe.

Discussion

The baseline surveys have established the initial conditions of the vegetation on the mitigation parcels. The five tree species that were detected at Pu`u Mali represent the majority of the native tree species expected in this region (Rock 1913). This suggests that existing seeds and scattered trees could result in forest regeneration at the local, if not landscape, scale. Individual trees were concentrated in localized patches within the `a`ā flow at Pu`u Mali, whereas Ka`ohe supported fewer tree species and they were generally more scattered and less abundant. Tree density was lowest on transect 101 at Ka`ohe, suggesting that habitat restoration in this parcel may take a long time without planting and active management. The disparity in tree distribution between the two mitigation parcels affords an opportunity to attempt different restoration techniques designed for the conditions at each site.

Invasive plants may impede native species recovery in both mitigation parcels. Although both areas have been invaded or are imminently threatened by relatively few habitat-modifying weeds, Kikuyu grass (*Cenchrus clandestinus*) is of particular concern because it forms large, nearly impenetrable mats of vegetation that hinder germination of native shrubs and trees. Other exotic species, such as cape ivy, gorse (*Ulex europaeus*), and banana poka, which are common on Mauna Kea in places outside of Palila Critical Habitat, could also negatively impact restoration efforts.

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27 WEED SURVEY IN PALILA CRITICAL HABITAT

Steve J. Dougill, Paul C. Banko

Introduction

Reflecting a long history of disturbance, 69% (125/180) of the plant species found in the subalpine forests of Mauna Kea are alien in origin (see Chapter 25: Vegetation Survey in Palila Critical Habitat), and the majority of these are invasive. Introduced ungulates have promoted the spread of alien plant species both in the Hawaiian Islands and on continents (Loope 1992). Introduced plants do not normally invade undisturbed Hawaiian ecosystems (Mueller-Dombois *et al*. 1981, Loope and Scowcroft 1985). Nevertheless, once they are established, many weed species do not disappear even after the disturbance factors are removed. In fact, many weeds continue to spread or are maintained because of natural disturbance factors. During the past 200 years, at least 861 alien plant species have become naturalized in Hawai'i, representing 47% of the total flora (Wagner *et al*. 1999). Perhaps 90% of alien plant species are of very little consequence in natural landscapes (Loope 1992). Nevertheless, 2% are considered serious threats to native ecosystems (Smith 1985, Wester 1992), and 150–200 species are thought to be causing ecological damage (Loope and Kraus 2009). This number is likely to increase with time as new species become established and naturalized species become more abundant and widespread.

Few studies in Hawai'i have addressed the distribution of alien plants through systematic, large-scale surveys. Most surveys have been conducted in response to localized management actions such as feral pig (*Sus scrofa*) removal (Stone *et al*. 1992), fire (Jacobi 1981, Tunison *et al*. 1994), or weed control (Tunison and Zimmer 1992). Nevertheless, as part of an island-wide bird and habitat survey conducted during 1976–1981, Jacobi and Warshauer (1992) mapped the distribution of six particularly noxious weed species using belt transects. We used a similar method in 1999 to determine the distribution of select invasive plant species and to evaluate their potential to impact the dynamics, structure, and restoration of Palila Critical Habitat (PCH) in the dry, subalpine zone of Mauna Kea. The palila (*Loxioides bailleui*) is an endangered Hawaiian honeycreeper that primarily eats the green seeds of native māmane (*Sophora chrysophylla*) trees, and it has become restricted to the southwestern slope of Mauna Kea (Banko *et al.* 2013). Therefore, much of our weed survey effort was concentrated in this portion of PCH. Another goal of the survey was to establish a baseline for assessing changes in alien plant distributions over time.

Our 1999 survey focused on 15 alien plant species that were considered a serious or potential threat to the dry forest ecosystem of Mauna Kea. These species can be categorized by their potential effects on the native forest and by their floristic affinities, as follows: 1) fire fuels and ground cover, 2) smothering vines, 3) competitive shrub, and 4) hosts for alien insects.

The relatively small number of extremely harmful weeds exert their influence by: causing declines in populations of native species, altering ecosystem processes, threatening neighboring agricultural lands, and damaging the aesthetic perception of the landscape (Loope 1992). The degree of threat posed by alien plants depends on their site-related impacts and their potential to colonize new areas.

Fire Fuels and Ground Cover

Sweet vernal grass (*Anthoxanthum odoratum*), orchard grass (*Dactylis glomerata*), velvet grass (*Holcus lanatus*), Kikuyu grass (*Cenchrus clandestinus*), fountain grass (*Cenchrus setaceus*), and Kentucky blue grass (*Poa pratensis*) are widespread and abundant introduced grasses on Mauna Kea. Māmane regeneration may be restricted by the dense ground cover of these species (Williams 1994, Hess *et al.* 1999). Additionally, the risk of intense, fast-moving fires is greatly increased by these grasses (Thaxton and Jacobi 2009). Fountain grass also has been recognized as a noxious weed by the Hawaiʽi Department of Agriculture (1978) and the National Park Service (1986). The herbaceous species fireweed (*Senecio madagascariensis*) is a recent but fast-moving colonizer that has spread from the Waimea pasturelands and, in addition to elevating the risk of fire (Thaxton and Jacobi 2009), is poisonous to livestock (Smith 1992, Motooka *et al.* 2004, Gardner *et al.* 2006).

Smothering Vines

Cape ivy (previously known as German ivy, *Delairea odorata*) and banana poka (*Passiflora tarminiana*) are invasive vines that are regarded as structural parasites because they reduce the photosynthesis of host trees. Banana poka was introduced into the Puʽu Waʽawaʽa area of Hawaiʽi in the early 20th century (Pung 1971) and has been subsequently spread by humans, other mammals, and birds throughout the islands. It occurs in the inter-mountain region between Mauna Kea and Mauna Loa and in the pasturelands on the northern slopes of Mauna Kea in what was native mesic māmane and koa (*Acacia koa*) forests. Banana poka can become a permanent component of the vegetation, causing loss of structural integrity and lowered species richness (Jacobi and Warshauer 1975, Burton 1980, Mueller-Dombois *et al.* 1980, La Rosa 1984, Jacobi and Scott 1985). Cape ivy is native to South Africa and was probably introduced to the leeward side of Hawaiʽi as an ornamental around 1909 (Haselwood and Motter 1983). It has become a conspicuous component of mid-elevation mixed māmane-naio (*Myoporum sandwicense*) forest on the western slope of Mauna Kea with smaller satellite populations establishing away from the main infestation.

Competitive Shrub

Gorse (*Ulex europaeus*) was inadvertently introduced before 1910 with the establishment of the wool industry in Hawaiʽi (Tulang 1992). Currently gorse is found in Humuʽula on the southeastern slope of Mauna Kea. It is a serious pest and one that is likely to encroach into PCH unless controlled.

Hosts for Alien Insects

Horseweed (*Conyza boniarensis*), stinking everlasting (*Helichrysum foetidum*), telegraph weed (*Heterotheca grandiflora*), mullein (*Verbascum thapsus*), golden crown-beard (*Verbesina encelioides*), and fireweed are invasive annual and perennial weed species. Most are found throughout the māmane forests of Mauna Kea, although telegraph weed and horseweed tend to be more abundant at lower elevations. Golden crown-beard is abundant in the inter-mountain saddle area and is likely to occur at lower elevations in the mixed naio-māmane forests. Mullein has been very effective in becoming established at high elevations, achieving serious pest status (Smith 1985). First established in the Kona district between 1900 and 1910, mullein spread to the saddle area by 1948 and was recorded above 3,290 m on Mauna Kea by 1980 (Juvik and Juvik 1992). Fireweed recently invaded Mauna Kea from adjacent range lands. In addition to other potential impacts, these weeds may provide a supplementary nectar source for introduced parasitic wasps and flies that parasitize the native caterpillars on which palila and other native birds feed (Brenner *et al.* 2002, Oboyski *et al.* 2004; see Chapter 19: Threats to

Food Resources: *Cydia* Caterpillar Parasitism and Chapter 20: Threats to Food Resources: Foliar Caterpillar Parasitism).

Methods

The 15 weed species were sampled during 1–9 June 1999 along 32 transects that encircled PCH (Figure 27.1). Trained observers slowly walked 15 m to either side of the center of each transect, looking closely for weeds. The presence of weed species was recorded at stations (*n* = 678) spaced at 150-m intervals along the transects. About one to two minutes were required to record data at each station. This method was employed in order to compare the distribution of some of the weed species recorded during the forest bird survey in 1981 (Scott *et al*. 1981, Jacobi and Warshauer 1992).

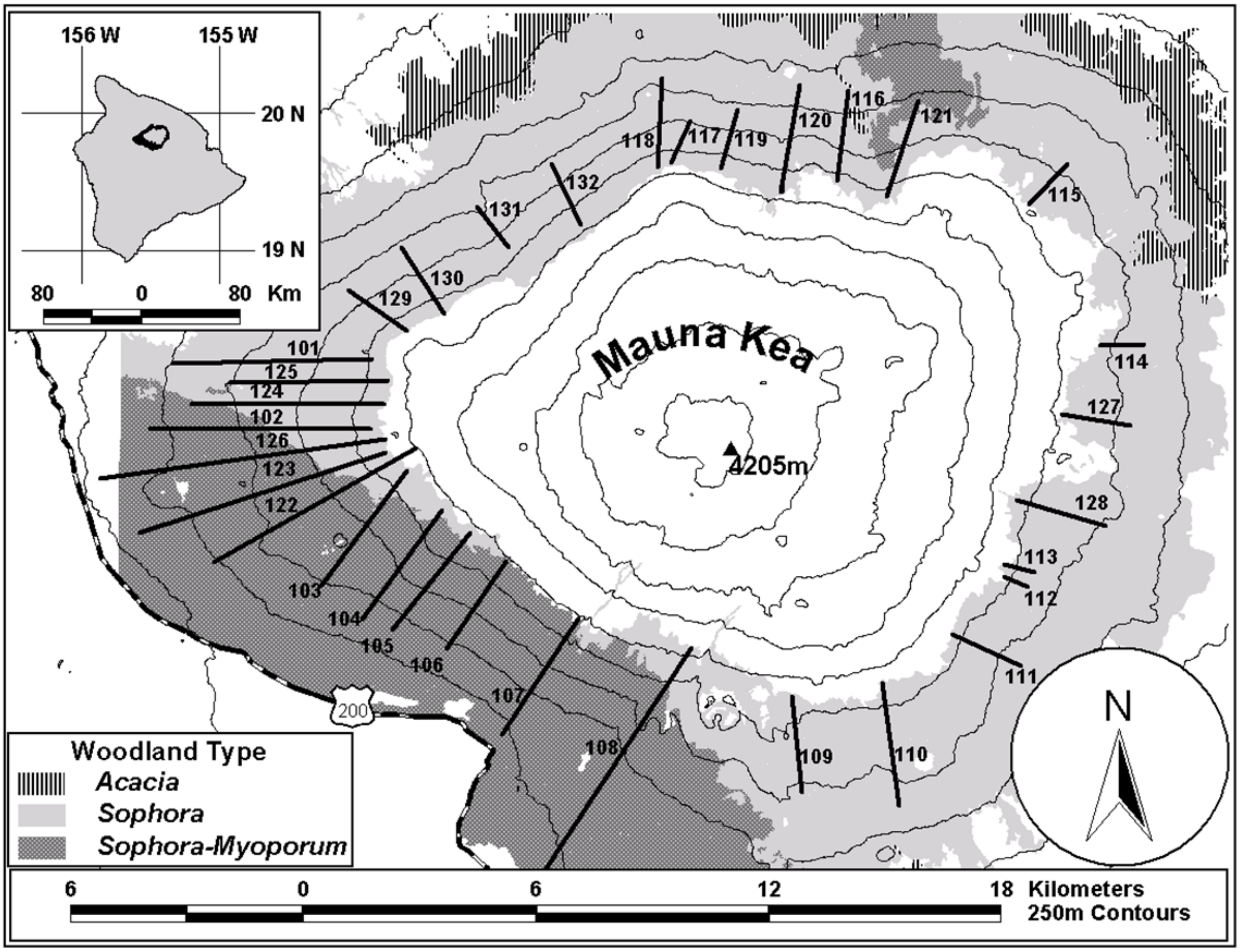

Figure 27.1. Locations of 32 weed survey transects on Mauna Kea Hawai‘i, February 1999–May 2001.

We also searched for weeds seen along roadsides and we opportunistically sampled additional points to identify outlying individuals or populations away from transects or roads. Using station data and these additional survey points, 75% kernel distributions (Worton 1989, Seaman and Powell 1996) were calculated using the Animal Movements Extension for ArcView GIS (Hooge and Eichenlaub 1997).

Results

We found 13 of the 15 targeted weed species on the survey transects. The 13 alien species were distributed on the western slope, and eight were also found on at least one other slope. No species occurred on all 32 transects, but five were recorded on 24 (75%) transects (Table 27.1). Gorse was not located on the survey, although it infested a large area of pastureland below PCH on the eastern slope of Mauna Kea. We did not detect golden crown-beard on the survey transects, but it was observed in several isolated populations along roadsides within PCH.

Table 27.1. Distribution of weed species on 32 survey transects in Palila Critical Habitat, June 1999.

	Distribution on slope	Number of transects where present	Number of transects with presence at >75% of stations	Number of transects with presence at >50% stations
FIRE FUEL AND GROUND COVER				
Anthoxanthum odoratum	W, N, E, S	29	20	22
Cenchrus setaceus	W	7	0	1
Dactylis glomerata	W, N, E	26	16	18
Cenchrus clandestinus	W	1	0	0
Holcus lanatus	W, N, E, S	30	22	22
Poa pratensis	W, N, E, S	24	10	15
Senecio madagascariensis	W, N	8	1	2
COMPETITIVE SHRUB				
Ulex europaeus	E[1]	0	0	0
SMOTHERING VINE				
Delairea odorata	W	5	0	2
Passiflora tarminiana	W	1	0	0
HOST FOR ALIEN INSECTS				
Conyza bonariensis	W, N, S	12	1	3
Helichrysum foetidum	W	11	1	3
Heterotheca grandiflora	W, N, S	17	8	10
Verbascum thapsus	W, N, E, S	28	18	25
Verbesina encelioides	W[2]	0	0	0

[1] Not found on transects but distributed widely across eastern slope below Palila Critical Habitat

[2] Not found on transects but found along roadsides in Palila Critical Habitat

Of the six grass species, we found sweet vernal grass, orchard grass, velvet grass, and Kentucky blue grass on at least 24 of the 32 transects, and they typically occurred at >50% of the stations on each transect. Although these species were widely distributed, they were not found on the southwestern slope (Figure 27.2). On the other hand, fountain grass was found only on the southwestern slope. We found Kikuyu grass only at survey stations in grazed, wooded pasture on the western slope at the edge of PCH.

Only two herbaceous species, mullein and telegraph weed, were present on more than half of the transects (Table 27.1). Mullein was scarce on the eastern slope (Figure 27.3), but it was found at most of the stations on the 27 transects on the other slopes. Telegraph weed was absent from the eastern slope, but it was frequently observed along the 17 transects where it was recorded. Horseweed, stinking everlasting, and fireweed were distributed on 8−12 transects primarily on the western slope, where they were encountered relatively infrequently.

Two individual banana poka plants were found on the western slope of Mauna Kea close to Puʽu Lāʽau Cabin on the edge of PCH in a cinder mining area (Figure 27.3). Both plants were destroyed to prevent their spread.

Cape ivy covered an area of 98.3 ha in the naio-māmane forest on the western slope between 1,750 and 2,250 m elevations (Figure 27.4). Small satellite populations at 2,640 m elevation in the pure māmane forest were uprooted to prevent further range expansion.

We recorded increases in the distributions of cape ivy and fountain grass since 1981 (Figure 27.5). Cape ivy was found at three stations on transect 102 in 1981 (Jacobi and Warshauer 1992), while we found it at 19 stations along transect 102 in 1999. Fountain grass was recorded at nine stations between transects 103–107 in 1981. In 1999, fountain grass was recorded at 26 stations, and it was also present on transect 101.

In addition to target species, we noted localized populations of other weeds that pose potential threats and warrant monitoring. Russian thistle (*Salsola tragus*), molasses grass (*Melinis minutiflora*), and prickly-pear cactus (*Opuntia ficus-indica*) were rare on the lower western slope, and California poppy (*Eschscholzia californica*) was restricted to two small populations at 2,790 m and 2,000 m elevation on the southern slope. More widely distributed were several grass species, including Natal redtop (*Melinis repens*), which was found on the lower southern and western slopes. It was also common in the disturbed area around Mauna Kea State Park. Perrenial ryegrass (*Lolium perenne*) and smutgrass (*Sporobolus africanus*) dominated many open areas in the lower naio-māmane forest on the western slope. Needlegrass (*Stipa cernua*) was common near tree line on the western and southern slopes and formed dense cover with purple veldtgrass (*Ehrharta calycina*) in Pōhakuloa Training Area near Mauna Kea State Park and along the lower portions of transect 108. Hairy oatgrass (*Rytidosperma penicillatum*) occurred over much of Mauna Kea, especially on the southern and western slopes. It was often the only alien grass on the southwestern slope between transects 104 and 107. Pepper grass (*Lepidium africanum*) formed the dominant ground cover in many high-elevation rocky areas on the western slope.

Discussion

Due to logistical constraints, the weed survey was designed to focus on a limited number of species. The 15 selected species represent those with the greatest potential for creating negative impacts in the native forest. Nevertheless, the effects of many of these weeds on regional hydrological processes, nutrient cycling, and native plant health are not well known.

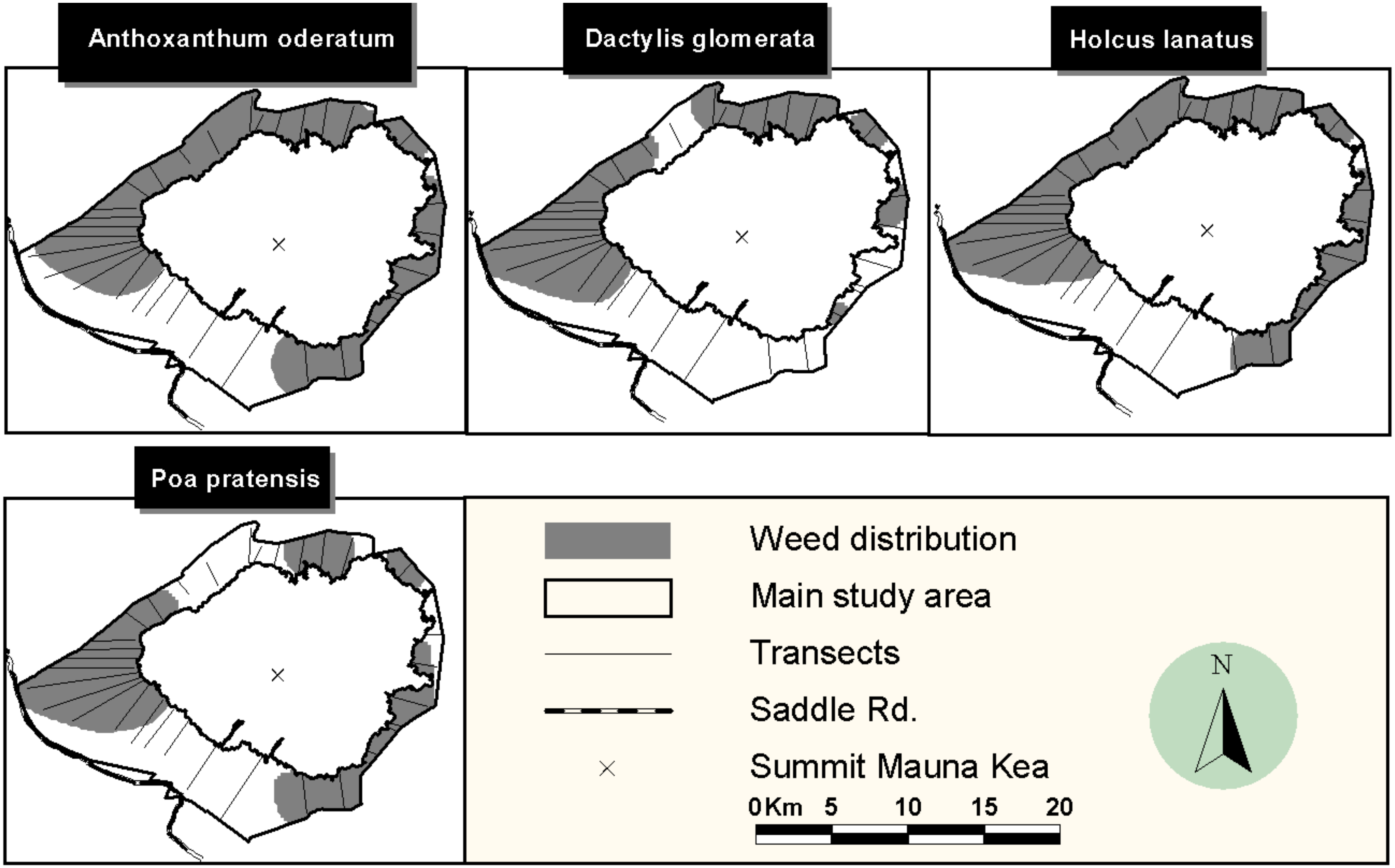

Figure 27.2. Distribution of four alien grass (weed) species on Mauna Kea, Hawai`i, June 1999.

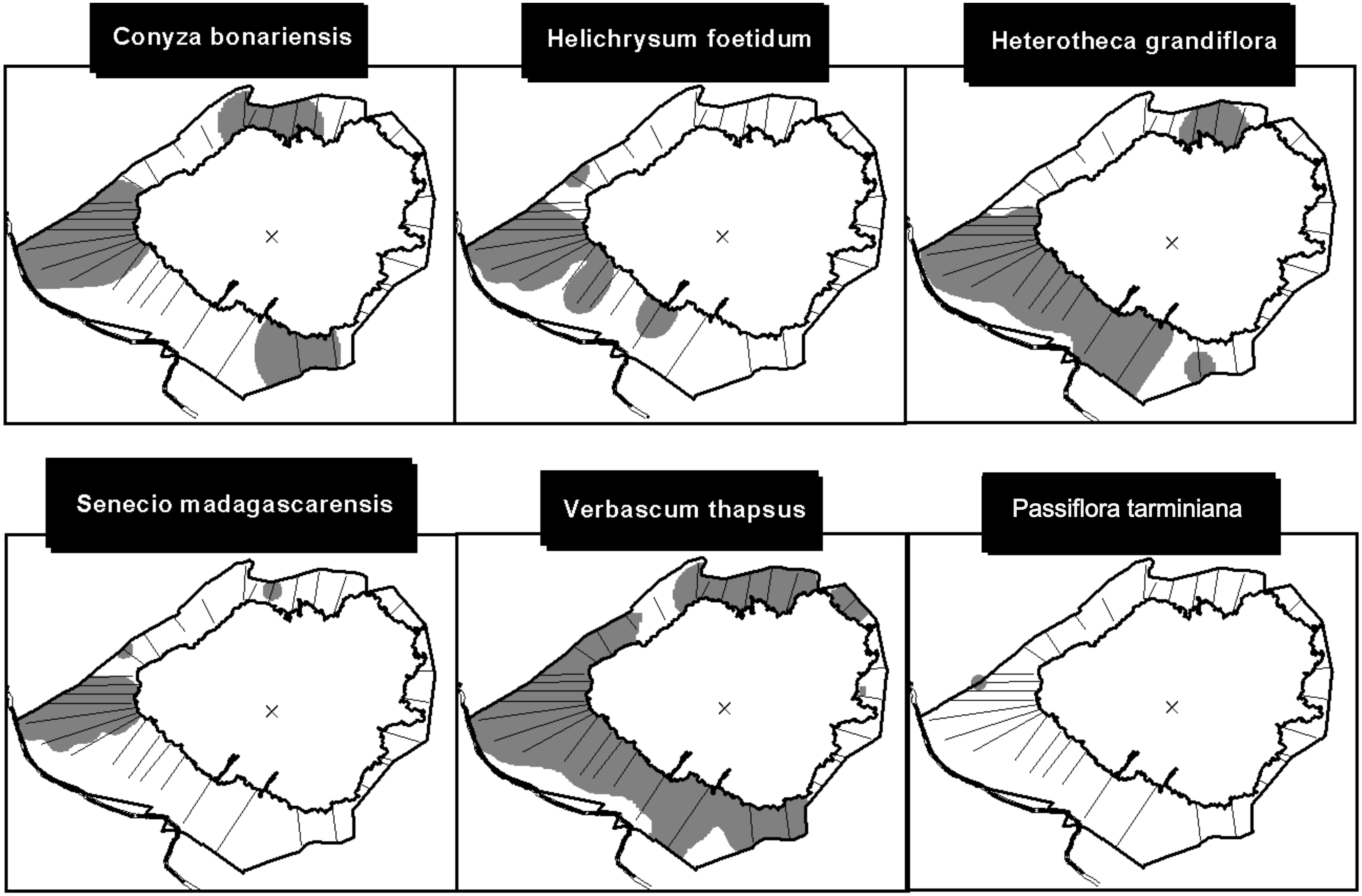

Figure 27.3. Distribution (gray area) of six alien plant species on study area transects on Mauna Kea, Hawai'i, June 1999.

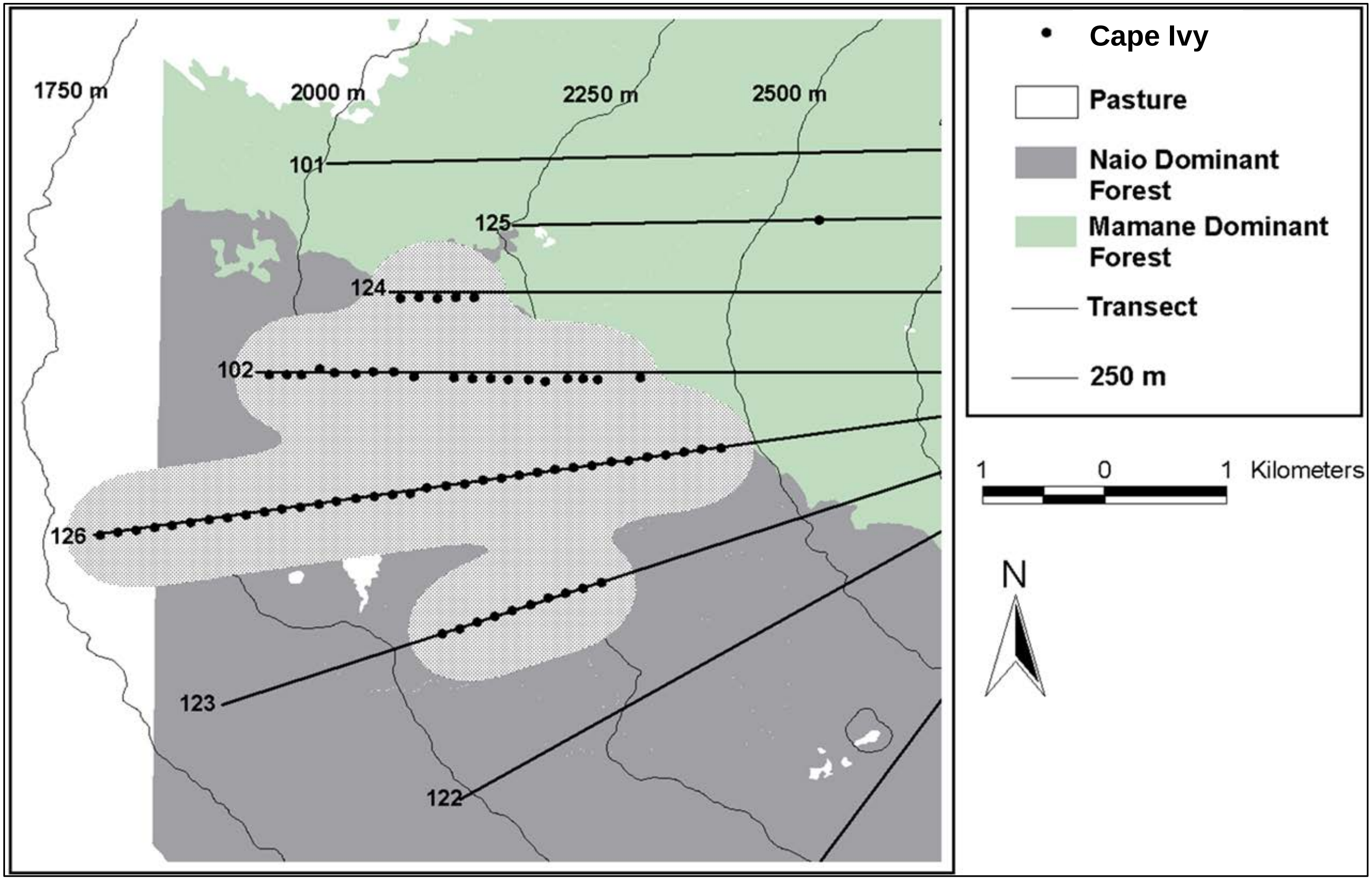

Figure 27.4. Distribution of *Delairea odorata* (cape ivy) on the western slope of Mauna Kea, Hawai'i, 1999. The gray cross-hatched area represents the 75% kernel probability distribution.

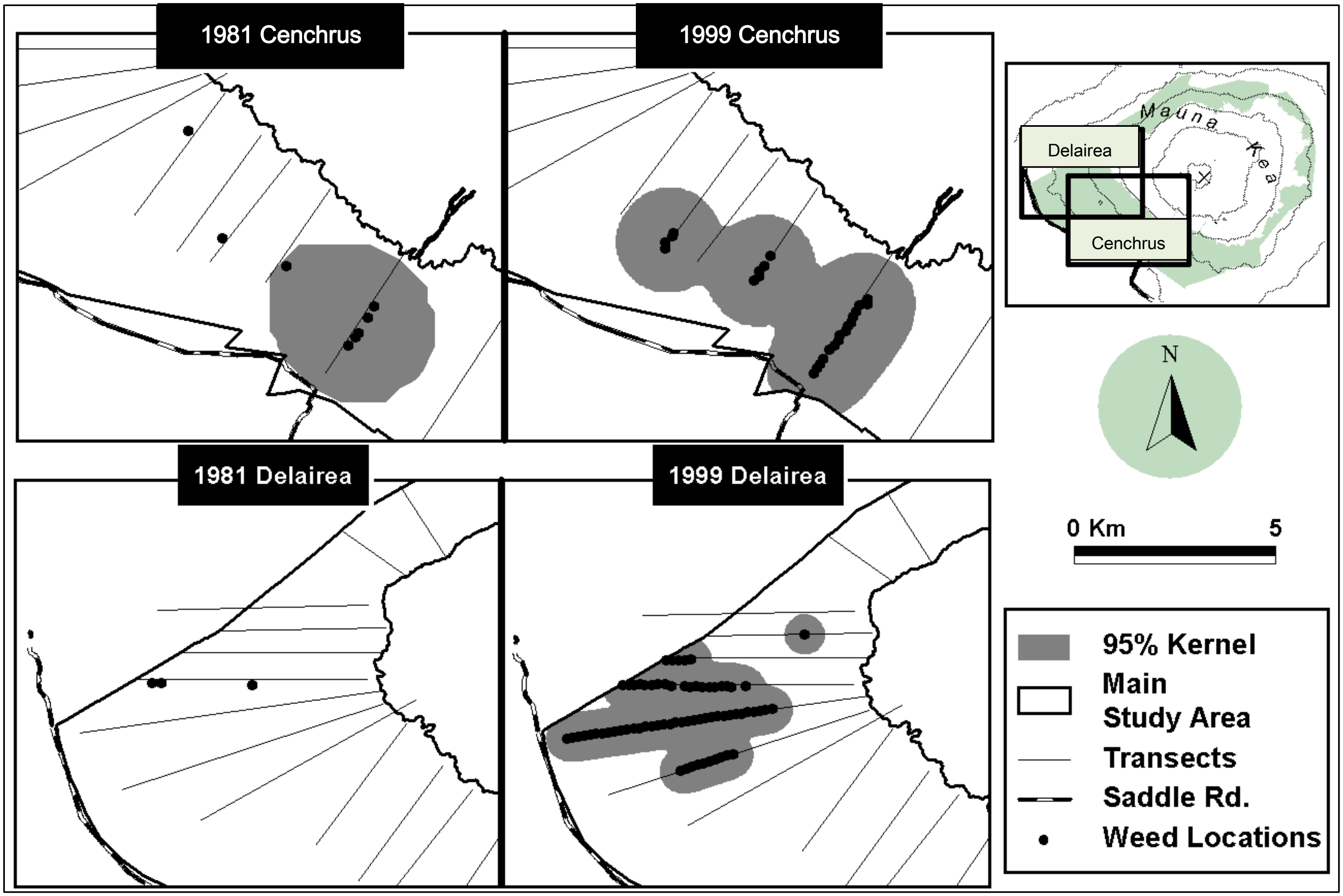

Figure 27.5. Distribution of alien *Cenchrus setaceus* and *Delairea odorata* on Mauna Kea, Hawai'i, in 1981 and 1999.

The species we chose also may have been biased towards weeds that were already abundant on the western slope of Mauna Kea, the core of the palila's range (Banko *et al*. 2013). For example, we did not record any target herbaceous species, except mullein, from the eastern slopes of Mauna Kea, yet gosmore and several clover species were common there and may negatively affect native species in some way.

Although we established a baseline for evaluating future changes in alien plant distribution, much of the history of individual species invasions is unknown. For example, we seldom know when a species invaded Mauna Kea, and we lack data on growth rates, fecundity, and spread under different environmental conditions. Most of the grasses we found are associated with cattle grazing, are widely distributed in Hawai'i, and may have been present for more than 150 years on Mauna Kea. Although many alien grass species have long been established and occupy nearly all available habitats on Mauna Kea, we have little information about their influence on fire regimes or other ecological processes.

As part of a vegetation survey of the upland regions of Hawai'i, Jacobi and Warshauer (1992) mapped the distribution of cape ivy and fountain grass on Mauna Kea. Using the same 17 transects and a similar sampling procedure, we were able to compare changes in the distribution of these two invasive weeds. Despite a large source population below PCH close to Saddle Road, the abundance of fountain grass increased only slightly during the 20-year interval, and it remained restricted to the lower southern and southwestern slopes. At a finer scale, several individual populations located in 1980 were absent in 1999; similarly, we discovered a small number of new populations that were not detected 20 years earlier. Nevertheless, the main fountain grass infestation occurred below the area sampled by either the 1980 or the 1999 survey; therefore, we are uncertain whether fountain grass was spreading upslope towards PCH. Although scattered, outlying populations seemed not to have persisted for a long time, new populations continued to colonize disturbed ground in the region. This grass was found mostly in small, disturbed sites, suggesting that native vegetation may replace fountain grass once disturbance from ungulates has been eliminated.

In contrast to the subtle changes in fountain grass distribution, cape ivy increased markedly since 1980. Although it remained concentrated on the lower western slope of Mauna Kea, it increased in the mixed naio-māmane forest. Satellite populations in the māmane forest at higher elevations were rare in 1999, but indicated potential for continued spread.

Fireweed was first detected in cattle pastures close to the town of Waimea in 1985 (Smith 1985). The species was not recorded in PCH until 1997, when it was noted as rare (U.S. Geological Survey unpublished data). Its spread since then has been explosive. We found fireweed at 10% of our transect stations in 1999, but by 2007 it occupied 86% of stations (n = 381) and had spread to tree line (U.S. Geological Survey unpublished data).

Fire

Wildfire has become a major agent of disturbance in dry Hawaiian ecosystems, where it may transform native-dominated forests and shrublands into alien-dominated grasslands (Hughes *et al*. 1991). Wildfires in Hawai'i increased in frequency, size, and intensity in the late 20th century due to the spread of invasive alien grass species (Cuddihy and Stone 1990, Smith and Tunison 1992). The spread of alien grasses has been facilitated by soil disturbance caused by feral ungulates and their preference for browsing native species (Scowcroft and Conrad 1992, Stone *et al*. 1992).

Many alien grasses feature fuel characteristics that escalate fire risk, and following fire they regenerate and spread rapidly, leading to grass/fire cycles that promote increased grass cover and fuel loading, changes in native plant community structure and composition, and invasions of additional weeds (Hughes *et al*. 1991, D'Antonio and Vitousek 1992, Smith and Tunison 1992). Therefore, having been invaded by fire-prone alien grasses that form dense, continuous fuel beds, the subalpine forest of Mauna Kea could be rapidly transformed to alien-dominated woodland or grassland by grass/fire cycles. Even without fire, invasive grasses may reduce growth and recruitment of native species, including māmane (Hughes and Vitousek 1993; Williams 1994; D'Antonio *et al*. 1998, 2000; Hess *et al*. 1999), and alter ecosystem processes (Mueller-Dombois 1973, Asner and Beatty 1996, Ley and D'Antonio 1998).

Wildfires probably occurred infrequently in subalpine Mauna Kea prior to human disturbance, although the fire history here and elsewhere in Hawaiʽi is poorly known. Lightning strikes would have been the major source of ignition prior to anthropogenic fires, such as military training at the adjacent Pōhakuloa Training Area, vehicle-related (catalytic converter) fires associated with roads, uncontrolled gorse burning, and arson. Although we do not know how native bunchgrasses were distributed prior to alien disturbance factors, the almost continuous cover of alien grasses that occurs today provides abundant fine fuel to sustain intense, fast-moving fires in many areas (Thaxton and Jacobi 2009).

Although widespread on Mauna Kea, orchard grass, velvet grass, sweet vernal grass, and Kentucky blue grass are rare or absent on the southwestern slope, which is largely dominated by dense naio stands at higher elevations and naio-ʽaʽaliʽi (*Dodonaea viscosa*) shrubland at lower elevations. Nevertheless, fountain grass occurs extensively on the southwestern slope and has the potential to begin a grass/fire cycle that would be difficult to break. The native bunchgrass, *Eragrostis atropioides*, also is common on the arid southwestern slope and flourished after wildfires in 1991 and 1995 that started along the road skirting the lower edge of the forest (U.S. Geological Survey unpublished data). Further research is needed to determine whether grass/fire cycles based on native grass species may develop on Mauna Kea.

Most of the grasses found on Mauna Kea likely increase the threat of fire, but fire hazard and impact escalate where grass densities are high and the fuel bed is continuous. Grass density is high over several extensive areas of the mountain: 1) mid elevations on the western and eastern slopes where orchard grass, velvet grass, sweet vernal grass, and Kentucky blue grass dominate; 2) lower elevations of the western slope where Natal redtop, perennial ryegrass, and smutgrass are common; and 3) low elevations on the southern slope close to Mauna Kea State Park, where needlegrass, purple veldtgrass, and fountain grass are abundant. Local conditions in each area also may affect fire behavior and impacts.

In addition to grasses, the dramatic explosion of fireweed around Mauna Kea has increased the fire hazard (Thaxton and Jacobi 2009). Several alien shrubs, most notably gorse and Russian thistle, also have the potential to change the fire regime, especially if they become more abundant and widespread. Although gorse was concentrated in alien-dominated pasture on the eastern slope, it has the potential to spread higher and into PCH. Forests in New Zealand may recover naturally as plants regenerate through gaps in senescing gorse stands (Gaynor and MacCarter 1981); however, this invasive shrub can affect biophysical conditions that inhibit native species establishment. For example, rainfall interception may reduce soil moisture under dense gorse stands, resulting in poor regeneration of native seeds during relatively dry periods (Richardson and Hill 1998). Furthermore, gorse has the potential to alter soil conditions by fixing nitrogen. This aspect of its ecology has not been investigated in Hawai'i, although native species adapted to nitrogen-poor soils suffer competitively from invasive nitrogen-fixers (Vitousek *et al.* 1987). Finally, the large monotypic stand of gorse on Mauna Kea is an extreme fire hazard (Motooka *et al.* 2003).

Although rare, Russian thistle spreads quickly and forms prickly, monotypic stands that burn easily and spread fire. It is a problematic weed throughout arid climates of western North America because of the ease with which the windborne seeds disperse and germinate after rain (Young 1991, Whitson 1999). It became established early in pastures below the māmane forest on the western slope, and it was first noticed in 1995 on the southern slope in Pōhakuloa Training Area, where control efforts have relied on herbicides (S. Evans, Colorado State University, personal communication). Generally, Russian thistle is present only through early successional stages where it invades barren desert areas and highly disturbed plant communities. Under some circumstances, Russian thistle can speed the rehabilitation of highly disturbed sites when this weed is left in place (Allen and Allen 1988, Grilz *et al.* 1988). We found and destroyed only a small number of individuals on the lower western slope of Mauna Kea.

Competition

A great variety of herbaceous weed species blanket PCH. Taken together, herbaceous weeds have considerable potential for displacing native species, although the competitive ability of individual species has not been evaluated. Two vines, cape ivy and banana poka, climb on trees and shrubs, thereby reducing the availability of light, competing for water and nutrients, breaking branches, and suppressing seedlings and saplings (Jacobi and Warshauer 1975, Burton 1980, Mueller-Dombois *et al.* 1980, La Rosa 1984, Jacobi and Scott 1985, Cuddihy and Stone 1990). Both species of vine spread when ungulates disturb the understory.

Banana poka was introduced into the Pu'u Wa'awa'a area of Hawai'i in the early 20th century (Pung 1971) and was subsequently spread by humans, birds, and mammals throughout the islands. Previous to our survey, the species had not been reported within PCH. The plants were found at Pu'u Lā'au, a location central to the western slope and representing the highest elevation reported for the species in Hawai'i. The two plants we found and destroyed were heavily laden with fruit that were partly eaten by birds and rodents. The occurrence of these two individual plants so far away from other known populations and in a highly disturbed site suggests dispersal by humans. Nevertheless, once established and producing fruit, birds or feral pigs could serve as dispersal agents.

Cape ivy was probably introduced to the leeward side of Hawai'i Island as an ornamental about 100 years ago (Haselwood and Motter 1983). It became a conspicuous component of mid-elevation mixed māmane-naio forest on western Mauna Kea with smaller satellite populations indicating its potential to spread. The seeds are small, light, and easily carried by the wind. Long distance dispersal is probably common, but establishment seems to be rare based upon the few satellite populations found during our survey. Nevertheless, these outlying populations have the potential to expand. Cape ivy is reportedly poisonous to some ungulates (National Park Service 1998), and we observed no signs of browsing or insect damage during the course of our survey. Our observations indicate that the vines may cover individual trees for over 10 years without killing them; nevertheless, tree vigor and reproduction seemed conspicuously reduced compared to non-infested trees. Cape ivy may also suppress seedlings of native species. Although the vines wilt and die during prolonged drought, such as occurred during 1998–2000, the extensive root system allows plants to quickly sprout when rainfall increases.

Pest Facilitation

Weeds also provide food and shelter for many alien invertebrates and some vertebrates, such as the house mouse (*Mus musculus*). Some weeds provide nectar that may help sustain introduced wasps and flies that parasitize the caterpillars of native moths (Brenner *et al*. 2002, Oboyski *et al.* 2004; see Chapter 19: Threats to Food Resources: *Cydia* Caterpillar Parasitism and Chapter 20: Threats to Food Resources: Foliar Caterpillar Parasitism) that are eaten by palila and other native birds. Invasive weeds also may facilitate the spread and sustain populations of other alien insects, such as predatory ants and wasps (Jervis *et al*. 1993, Idris and Grafius 1995), but studies are needed to evaluate interactions between weeds and pests on Mauna Kea.

Mullein was the only target herbaceous species we found on the eastern slope of Mauna Kea. Nevertheless, gosmore (*Hypochoeris radicata*) and several clover species (*Trifolium* spp.) were widespread and common, and both might provide nectar for invertebrate pests. Additionally, in 1999 the Big Island Invasive Species Committee (a partnership of government agencies, organizations, and citizens) identified the California poppy as a weed of concern. This species occurs as a small population at Halepōhaku on the southern slope. It forms extensive stands in dry communities in the western United States, where it is native, suggesting that it could spread in the dry subalpine environment of Mauna Kea.

Management Implications

Eliminating or controlling weeds in PCH may speed habitat recovery, but more information is needed to demonstrate both the severity of impacts of particular species on the native vegetation and the feasibility of control measures. Many weeds are likely to persist a long time on Mauna Kea, and reducing the consequences of weed invasions may be a more realistic goal than control. For example, since subalpine Mauna Kea is dry with a year-round fire season, fire prevention and suppression and fuel management through the establishment of fuel breaks is needed until tree cover has increased sufficiently to reduce the density of fine, herbaceous fuels (Thaxton and Jacobi 2009).

Eliminating habitat disturbance by feral ungulates is a critical step towards forest recovery in PCH and elsewhere in Hawaiʽi (Loope and Scowcroft 1985, Banko *et al*. 2009). Efforts to eradicate feral sheep (*Ovis aries*), mouflon sheep (*O. gmelini musimon*), and goats (*Capra hircus*) were begun by the Hawaiʽi Division of Forestry and Wildlife in 1980, and māmane and other native plants are beginning to recover (Hess *et al*. 1999, Banko *et al*. 2009). Feral pigs will continue to be managed for sport hunting, although their digging creates favorable conditions for weeds while reducing native plant density (Spatz and Mueller-Dombois 1975) and is widespread in PCH (see Chapter 25: Vegetation Survey in Palila Critical Habitat).

Although many alien plant species are beyond control, others with small, localized populations might be eliminated through herbicide treatment or hand-pulling. Small populations of banana poka, Russian thistle, California poppy, prickly-pear cactus, and coffeeberry (*Rhamnus californica*), all of which have potential for rapid spread and significant impacts on native vegetation, could be eliminated from PCH with prompt attention and regular surveillance for new populations.

It may be possible to stop the spread of some species by eliminating satellite populations. We removed patches of cape ivy by hand at a number of locations above the main infestation on the western slope of Mauna Kea, and these sites were not recolonized even after several years.

Biological agents may also prove useful in controlling some weed species in PCH. Species targeted for biological control are gorse (Markin *et al.* 1996), fireweed (Ramadan *et al.* 2011), and banana poka (Ramadan *et al.* 2008). Lepidoptera are the principal agents being released, and the moth released for fireweed control may also feed on cape ivy in the wild, as it does under quarantine conditions (M. Ramadan, Hawai'i Department of Agriculture, personal communication). Other insects are also being tested against these and other weed species.

To limit the impacts of new weeds in PCH it is important to prevent their establishment. Weeds invade above tree line on Mauna Kea, and even the summit area (4,000 m) is vulnerable. In these extreme environments, native plants may be especially sensitive to even low densities of weeds. Precautions and monitoring during the construction of firebreaks, fences, and game bird watering units, would help to reduce the inadvertent introduction of weeds. Although poorly documented, some alien plants, such as coffeeberry and several grass species, were apparently introduced as supplemental food resources for game birds (L. Pratt, U.S. Geological Survey, personal communication). Given the long history of Hawaiian forest bird habitat destruction and degradation due to a diverse suite of invasive threats (Pratt and Jacobi 2009), the consequences of introducing alien plants in or near PCH should be carefully considered.

A monitoring program would provide information about the rate at which alien species are spreading in PCH and would better identify weeds that might seriously threaten native species and communities. Our survey was designed to provide a quick assessment of the distribution of select weeds and can be easily repeated, as we did in 2007 to document the rapid spread of fireweed. As the subalpine forest recovers from long-term ungulate damage, it will be helpful to anticipate changes in community structure and composition and interactions between native and alien species. Monitoring and research may reveal that some alien plants benefit native communities by preventing soil erosion and providing hospitable microhabitats for native seedlings and invertebrates. On the other hand, control strategies and management capacity are needed for species that clearly threaten PCH. Tree planting and other efforts to restore the forest may be most effective in reducing weed populations and may be necessary to reestablish native species in sites dominated by alien grasses. Grasses and other weeds may be inhibited where tree canopies substantially reduce light availability at ground level and produce sufficient litter accumulation (Thaxton and Jacobi 2009). Forest restoration can be promoted by reducing disturbance by ungulates, fire, and human activity.

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28 WEED SURVEY ON SOUTHWESTERN MAUNA KEA

Steve J. Dougill, Paul C. Banko

Introduction

Weeds that become abundant and widespread may threaten the subalpine dry forest that supports palila (*Loxioides bailleui*) and other native species. Weeds potentially compete with native plants for vital resources such as light, space, water, nutrients, and pollinators. They may also alter soil conditions to the detriment of native species. In addition, weeds may provide nourishment to populations of alien pests, thus allowing them to persist and increase in numbers. Perhaps the most serious consequence of weeds in palila habitat is the promotion of fire.

Weed distributions have been determined from surveys conducted in June 1999 along 32 Hawai'i Forest Bird Survey (HFBS) transects distributed around Mauna Kea (see Chapter 27: Weed Survey in Palila Critical Habitat). Although this framework allows us to assess environmental factors relevant to palila, many weed species occur below those transects and may spread into Palila Critical Habitat. This is especially true of fountain grass (*Cenchrus setaceus*), which is widely distributed between Mauna Kea and Mauna Loa (Shaw 1997). For these reasons we conducted surveys in the area between Saddle Road and the lowest extent of our primary transects on the southern and western slopes of Mauna Kea to evaluate the threat of invasion of weeds into palila habitat.

Three particularly noxious weed species were selected as the focus of this survey because of the threats they pose to the forests of Mauna Kea and the ease of their identification. We targeted fountain grass, cape ivy (*Delairea odorata*), previously known as German ivy, and prickly pear cactus (*Opuntia ficus-indica*) in the survey. Prior to 1949, prickly pear cactus spread rapidly on the island of Hawai'i, densely covering many lowland sites and spreading into upper elevations and pastures (Davis *et al.* 1992). Through a combination of biological control agents, the pest was brought under control and eliminated in many areas. Although currently rare within the subalpine forests of Mauna Kea, prickly pear remains a concern to managers despite earlier success with biocontrol (Davis *et al.* 1992). Biological agents also are being investigated to control cape ivy, an ornamental vine native to South Africa and introduced to Hawai'i Island over 100 years ago (Haselwood and Motter 1983). It has since become a conspicuous component of mid-elevation forest on the western slope of Mauna Kea with smaller satellite populations establishing away from the main infestation (see Chapter 27: Weed Survey in Palila Critical Habitat).

Methods

Weed surveys were conducted in November 1999 along transects used for mapping ant distributions, which included portions of some HFBS transects in Palila Critical Habitat (see Chapter 22: Threats to Food Resources: Ants). We used methods from our June 1999 weed survey (see Chapter 27: Weed Survey in Palila Critical Habitat) to record the presence of the three target weed species within a 30-m-wide strip along the transects, which extended upslope (east or northeast) from about 1,700 m elevation along Saddle Road to 2,900 m elevation near tree line, all on the southwestern slope of Mauna Kea. Transects were spaced 500 m apart along Saddle Road and the spacing narrowed to 200 m upslope. A total of 365 stations were located at 200-m intervals along the transect to provide spatial reference for recording the distribution of weed species (Figure 28.1). In addition to recording the presence or absence of

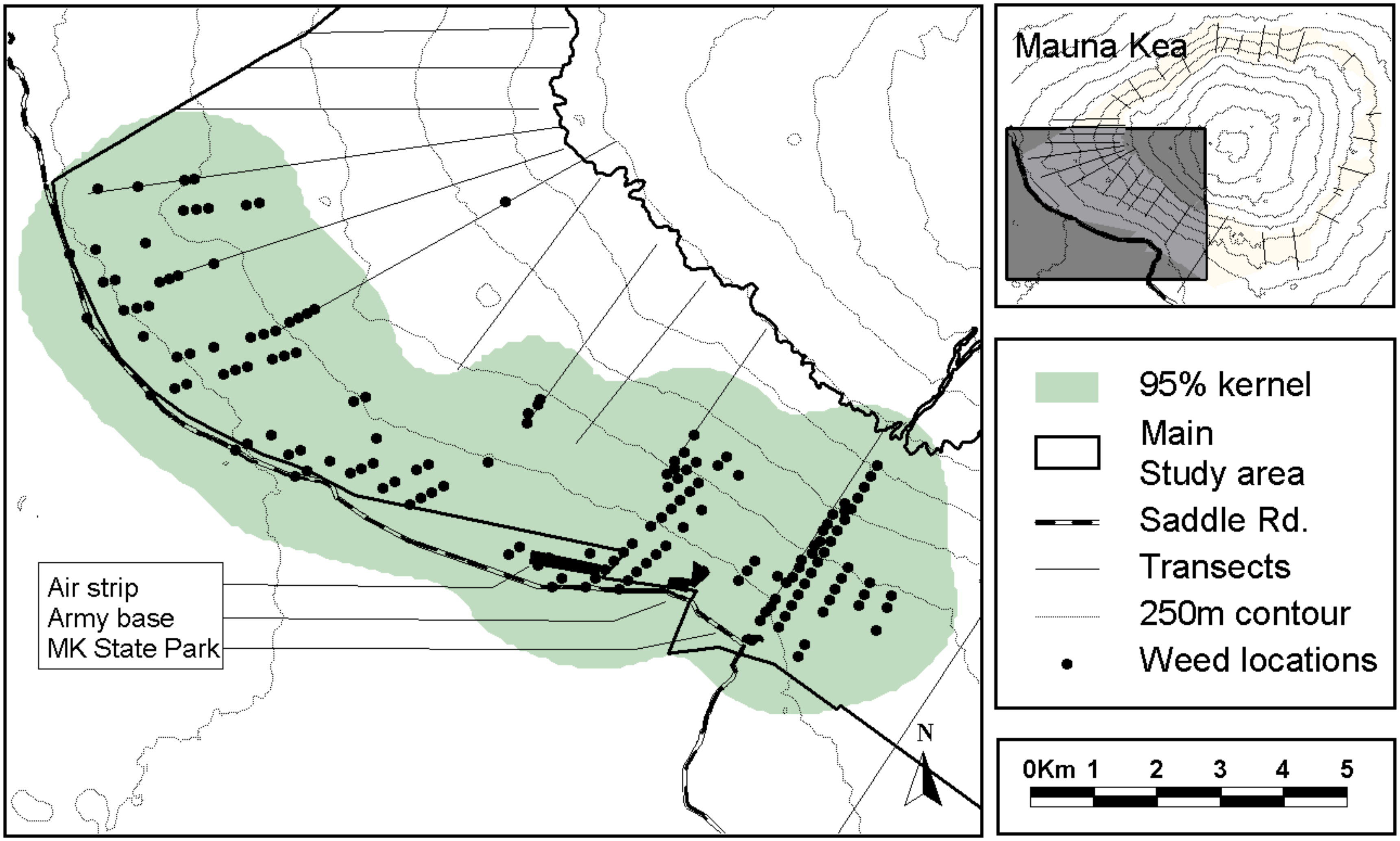

Figure 28.1. Distribution of *Cenchrus setaceus* grass on the western slope of Mauna Kea, Hawai`i, November 1999.

the target species, we recorded evidence that the site had been disturbed or was associated with roads, gullies, and other landscape features that would facilitate weed dispersal.

Results

We detected cape ivy at 19% of the stations (70/365), all on the western slope of Mauna Kea. Cape ivy occurred on the majority of stations along HFBS transects 102, 126, and 123 and was scattered along other western transects (Figures 27.4 and 27.5 in Chapter 27: Weed Survey in Palila Critical Habitat). Prickly pear was detected only as one large individual within Mauna Kea State Park. Fountain grass was found at 34% of the stations (125/365; Figure 28.1). The three weed species were nearly always found at disturbed sites or where dispersal could have been facilitated by water runoff, ungulates, or human activity. Sites with fountain grass were associated with gullies (small ravines) in 58% (54/93) of all locations (Table 28.1).

Table 28.1. The number of survey stations where fountain grass was detected and the landscape features associated with these sites. "No association" indicates that none of the four disturbance types was present.

Airstrip	Gully	Pu'u	Road	No association	No data
16	54	2	12	9	22

Discussion

Our survey revealed isolated patches of cape ivy outside the main concentration on the western slope. Cape ivy generally spreads vegetatively via a mass of fleshy roots and rhizomes. In California, where flowering has not been documented, disjunct populations have become established solely from the transmission of small pieces of plant material (Alvarez and Cushman 1997, California Exotic Pest Plant Council 1999). Nevertheless, viable seeds are produced in Manukā Natural Area Reserve, Hawai'i (J. Balciunas, U.S. Department of Agriculture, personal communication), and cape ivy flowers profusely on Mauna Kea in wetter years, offering an additional mechanism for windborne seed dispersal.

The patch of cape ivy close to HFBS transect 105 was growing in a very dry 'a'ali'i (*Dodonaea viscosa*) shrubland with scattered short trees, suggesting that the potential for invasion in many parts of Mauna Kea is high. Several isolated patches were also identified in pure māmane forest on the western slope in the June 1999 weed survey (see Chapter 27: Weed Survey in Palila Critical Habitat). Furthermore, the problem was not confined to the western slope; a small, but significant clump was noticed on the northern slope in a gully between HFBS transects 116 and 121 in March 2000 (U.S. Geological Survey unpublished data). Cape ivy dies back considerably during drought, but individual plants sprout rapidly from rootstock when rains return, suggesting that this weed poses a long-term threat to Palila Critical Habitat.

Although we encountered only one prickly pear cactus during our survey, a number of other individuals are known to occur on the southern and western slopes. Three small patches have been identified on Pu'u Ahumoa, and two individuals were found upslope of Bradshaw Airfield within Pōhakuloa Training Area. Attempts to manage small, scattered populations of the prickly pear (Davis *et al.* 1992) suggest that these biocontrol agents may not be effective until the host plant becomes abundant and may be already impacting the plant community.

Fountain grass was widespread on the lower southwestern slopes of Mauna Kea below the HFBS transects, and we found small patches and isolated plants within Palila Critical Habitat. Although fountain grass was encountered at about one-third of all stations in this survey, it was recorded in low densities (often as individuals or small clumps). It was distributed patchily, and most plants were associated with disturbance or a landscape feature that could act as a dispersal corridor. Its strong association with gullies offers a possible explanation for its spread. Gullies may facilitate dispersal and establishment by acting as wind corridors that funnel seeds from source plants. Gullies may also create new substrate for seeds in the disturbed soil of rock falls and landslides.

Fountain grass has probably been established longer near Mauna Kea State Park, where Jacobi and Warshauer (1992) found the lower half of HFBS transect 107 to be infested. By 1999 it had spread, becoming a common component of the vegetation along the lower southwestern slope (see Chapter 27: Weed Survey in Palila Critical Habitat). In some areas it was abundant and no longer exclusively associated with overtly disturbed substrates. Eliminating disturbance from introduced ungulates may reduce the potential for spread to higher elevations.

Because banana poka (*Passiflora tarminiana*) and Russian thistle (*Salsola tragus*) were found in small, isolated patches during weed surveys in Palila Critical Habitat in June 1999 (see Chapter 27: Weed Survey in Palila Critical Habitat), we returned to these sites to ensure that they were not becoming established. The site where banana poka was discovered (and removed) near Puʻu Lāʻau in June 1999 was monitored frequently in the following months to ensure that the plants were not reestablishing there. In February 2000, another plant was discovered and removed at the same location. Several specimens of Russian thistle, a weed that had been previously confined to Pōhakuloa Flats, were discovered on lower Skyline Road on the western slope of Mauna Kea in February 2000. Russian thistle is a problematic weed throughout arid climates of western North America because of the ease with which seeds spread and germinate. Seeds are windborne and germinate readily after only small amounts of precipitation (Whitson 1999). Once established, Russian thistle is notoriously difficult to eradicate because of its persistence in the seed bank. The population we found on Mauna Kea was removed by hand and monitored frequently for several years to prevent establishment.

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29 FIRE ECOLOGY

Steve J. Dougill, Paul C. Banko

Introduction

Fire management is a key issue for land managers protecting the palila (*Loxioides bailleui*) in subalpine Mauna Kea. The forest composing Palila Critical Habitat (PCH) is dry with a year-round fire season. At mid-elevations on the eastern and western slopes, alien grasses form an almost continuous ground cover, which greatly increases the threat of frequent, intense fires. Additionally, steep topography and daytime upslope winds raise the fire hazard. Natural fires are rare due to the low frequency of lightning in the area (Wakida 1997). Nevertheless, anthropogenic ignition sources are common and include military activities at Pōhakuloa Training Area, vehicles (catalytic converters), careless human activity, and uncontrolled gorse (*Ulex europaeus*) burning.

Since 1972, 10 of the 22 fires documented on Mauna Kea have burned within PCH (Wakida 1997). Many additional fires have been ignited in an effort to control gorse on the eastern slope of Mauna Kea (Wakida 1997). The two largest fires within Ka'ohe Game Management Area were started by vehicles: 1,230 ha burned in February 1978 and 469 ha burned in August 1990. There is no documentation of fires on Mauna Kea before 1972. Nevertheless, there are anecdotal accounts of large uncontrolled fires on the northern slope of Mauna Kea during the 1800s, presumably intended for pasture improvements. We initiated a study of the Pu'u Loa fire to better understand the effects of fire on the vegetation of subalpine Mauna Kea.

The Pu'u Loa fire was reported on the morning of 23 May 1999 in remnant māmane (*Sophora chrysophylla*) forest within pastureland leased for cattle grazing on the eastern slope of Mauna Kea. The fire was believed to have been started by a lightning strike between Pu'u Kole and the border of Mauna Kea Forest Reserve (forest reserve) at about 2,400 m elevation. The Hawai'i Fire Department (HFD) extinguished the fire after it had burned 8.9 ha of wooded pastureland. The fire rekindled on 1 June 1999 and spread upslope toward the forest reserve. A total of 28 fire fighters from Hawai'i State Division of Forestry and Wildlife and HFD extinguished the fire after an additional 24.3 ha burned, including a small area of forest. Two weeks later, hot spots were still smoldering, and it was apparent that the fire had burned unevenly and with varying intensities.

Methods

We mapped the boundary of the Pu'u Loa fire during 10–18 April 2000 and calculated the area to be 5.6 ha using a GPS with 5-m accuracy. We visited all trees within the burn to evaluate the effects of fire on mortality and the number of regenerating ground and epicormic (growing from underneath the bark of a trunk, stem, or branch) sprouts. These data were compared to trees within an adjacent control area that did not burn, located 20–100 m outside the boundary of the fire. To assess the effects of fire on community structure and individual tree characteristics, as well as the amount and type of regeneration, we employed a series of 0.04 ha circular plots (11.3-m radius). Due to the relatively small and linear shape of the burn, we selected a random sample of circular plots to sample the vegetation. A 20-m buffer was selected within the boundary of the fire using ArcView GIS to minimize edge effects. Within the burned pasture, we randomly selected nine plots with centers ≥40 m apart. Although little of the forest reserve burned (0.85 ha), we situated four plots within the affected area. To increase sampling effort, the 20-m buffer was relaxed in this area, although plot centers were separated by at least 40 m (Figure 29.1).

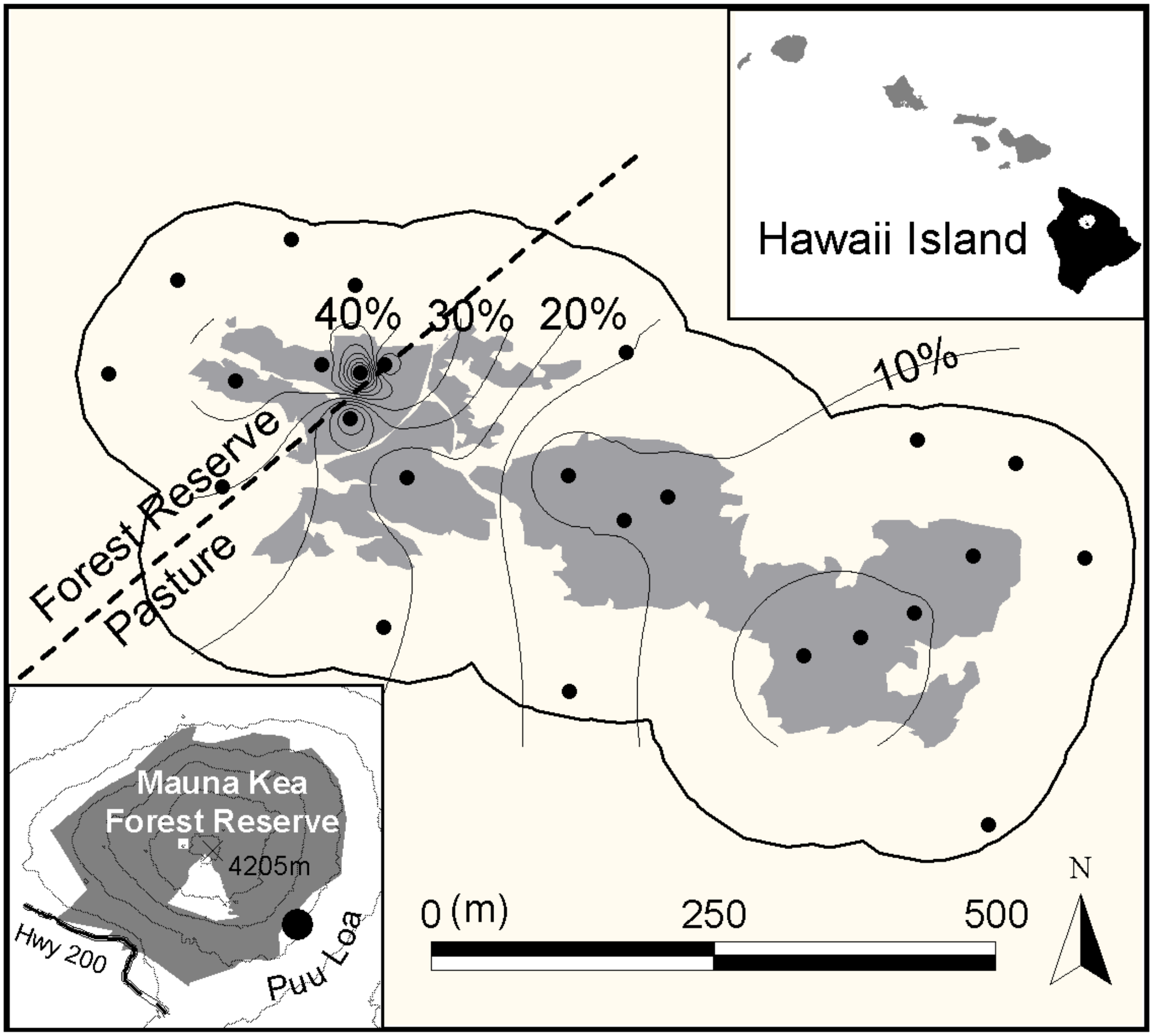

Figure 29.1. Sampling locations and fire intensity at Pu'u Loa (black dot in inset map) near the Mauna Kea Forest Reserve, Hawai'i, April 2000. Plot locations are indicated by black dots; grey areas designate locations affected by fire; and isohyets specify percent of vegetation that burned.

We have no data on the vegetation before the fire. Accordingly, to estimate the effects of fire on the vegetation in each habitat type, we compared the characteristics of plots in burned versus unburned forest reserve and burned versus unburned pasture. Thus, control plots were selected (eight in pasture and four in the forest reserve) in a zone between 20 and 100 m outside the boundary of the fire. The center of each plot was located ≥40 m from the next.

Plots were marked with a PVC pipe and metal tag for future monitoring. We sampled ground vegetation (results not reported), tree characteristics, and regeneration within each plot.

Community Composition and Fire Intensity

Two tape measures (marked in 1-cm graduations) were laid out perpendicular to each other in the four cardinal directions, crossing at the plot center. Plots were sampled by nine 1-m^2 quadrats. One was placed at the center (the top right corner of the quadrat placed against the center of the plot when facing upslope). Two quadrats were placed at random distances along each line (the top left corner of the quadrat placed at the randomly selected point on the line facing away from the plot center). Each quadrat was held roughly perpendicular to the ground with PVC pipe legs. A quadrat was repositioned with a different random distance if it was found to fall on a small cliff face or on a tree. The quadrats were made from ½" PVC pipe joined to form a 1-m square, subdivided into 10-cm squares with fine string. The intersection of these string lines created 81 points. A fine stiff wire was dropped at each of these points, perpendicular to the quadrat, to record the vegetation or coverage at the ground level. Only one species could be recorded for each point. In addition to the identification of the ground layer, we also recorded signs of burning at that point. Percentages of charred ground were used to calculate fire intensity with ArcView GIS (ESRI 1996).

Regeneration

Each plot was systematically searched for māmane saplings or suckers for at least 10 minutes by two people. The height of saplings that were growing at least 1 m away from the base of a māmane tree (alive or dead) were measured perpendicular to the ground and their diameters were measured with calipers at ground level. Individuals that were located within 5 cm of each other were considered one sapling, and the number of stems was counted. Similar variables were collected on suckers within 1 m of the base of a māmane tree.

Trees

Eight live trees were selected from each plot in the control areas and burned pasture using random direction vectors and distances. The closest two trees in the four quadrants were tagged for future monitoring. Because so little of the forest reserve burned, we were able to characterize in detail all live trees in this area. The following variables were measured: height and width of the tree; canopy density (the percentage of area that was obscured by foliage); vigor (the percentage of twigs with live foliage); diameter of the main trunk in centimeters at 10 cm above ground level; maximum height that charring was detected; number of sprouts <1 m tall growing from the trunk of the tree; and number of ground sprouts growing within 1 m of the base of the tree. We also assessed the phenology of the sample of trees with our standard methods (see Chapter 16: Food Availability: Māmane Phenology and Cydia Caterpillars).

Results

The burn was most intense in and near the forest reserve (Figure 29.1), and more dead trees were observed in the burned area than in the control area ($\chi^2 = 55.6$, $P = 0.01$). We used TWINSPAN (Hill *et al*. 1975, Gauch and Whittaker 1981) to assess the similarities among different plots. At the first ordination level, most of the plots within the unburned forest reserve were isolated as different (eigenvalue = 0.1557, $n = 4$). This result suggests that 15.6% of the variation was sufficiently similar to be grouped together by this ordination technique. These plots had high levels of *Holcus lanatus* and *Anthoxanthum odoratum* and low densities of *Poa pratensis*, *Festuca rubra*, and *Deschampsia nubigena*. Otherwise the plant communities varied little with respect to burn characteristics or land use. At the species level, pūkiawe (*Leptecophylla tameiameiae*) showed no signs of regeneration. On the other hand, vigorous root suckering was observed in ʽōhelo (*Vaccinium reticulatum*), bracken fern (*Pteridium aquilinum decompositum*), and *Dryopteris wallichiana* 10 months after the fire. The fire apparently caused little mortality in pasture trees because there was no significant difference in the numbers of dead trees in the burned versus unburned pasture.

To approximate conditions before the fire, we compared regeneration in the unburned forest reserve to regeneration in the unburned pasture. Significantly more suckers were counted in the forest reserve than in the pasture (ANOVA $F_{1,\ 1694}$ = 132.5, $P < 0.001$). At least one sucker was observed on 38.6% of trees in the forest reserve compared to only 8.1% of trees in the pasture (Table 29.1). Epicormic sprouting in control areas showed the same trend: 29% of trees in the forest reserve showed epicormic sprouting, as opposed to 14.1% of trees in the pasture (ANOVA $F_{1,\ 1694}$ = 13.9, $P < 0.001$; Table 29.1).

Table 29.1. Baseline calculations of regeneration in the unburned Mauna Kea Forest Reserve versus the unburned pasture (means ± SE).

Land use	Trees with suckers	Trees with epicormic sprouts
Forest reserve	38.6% (2.96 ± 0.27)	29% (1.23 ± 0.14)
Pasture	8.1% (0.468 ± 0.01)	14.1% (0.65 ± 0.08)

Compared to control plots, ground suckers associated with defoliated trees were more abundant in both the pasture (ANOVA $F_{1,\ 190}$ = 6.19, $P = 0.013$) and the forest reserve (ANOVA $F_{1,\ 190}$ = 3.49, $P = 0.063$; Table 29.2). Suckering was not significantly different ($P > 0.6$) on burned and unburned foliated trees within the forest reserve, but more suckers were recorded on burned trees than on control trees within the pasture (ANOVA $F_{1,\ 963}$ = 11.2, $P < 0.001$; Table 29.3). Additionally, more saplings were found in the burned pasture plots ($n = 11$) compared to the unburned plots ($n = 28$). These saplings were at least 1 m away from the base of a māmane tree and presumably represented regeneration from seed.

Table 29.2. Percentage of defoliated trees with ground suckers (means ± SE).

Treatment	Bare trees with ground suckers
Forest reserve/ control	11.6% (0.74 ± 0.40)
Forest reserve/ fire	20.7% (2.72 ± 0.75)
Pasture/ control	1.1% (0.06 ± 0.03)
Pasture/ fire	21.8% (1.42 ± 0.13)

The average number of flowers per tree was greater in the unburned areas (ANOVA $F_{1,\ 202}$ = 14.23, $P < 0.001$) and in the forest reserve (ANOVA $F_{1,\ 202}$ = 3.46, $P = 0.02$). There was no detectable difference in the number of pods ($P > 0.6$). The prevalence of flush was similar in the burned and unburned areas (Figure 29.2).

Table 29.3. Percentage of foliated trees with ground suckers (means ± SE).

Treatment	Foliated trees with suckers
Forest reserve/ control	43.6% (3.38 ± 0.31)
Forest reserve/ fire	26.0% (2.46 ± 0.99)
Pasture/ control	15.9% (0.936 ± 0.15)
Pasture/ fire	32.9% (2.06 ± 0.32)

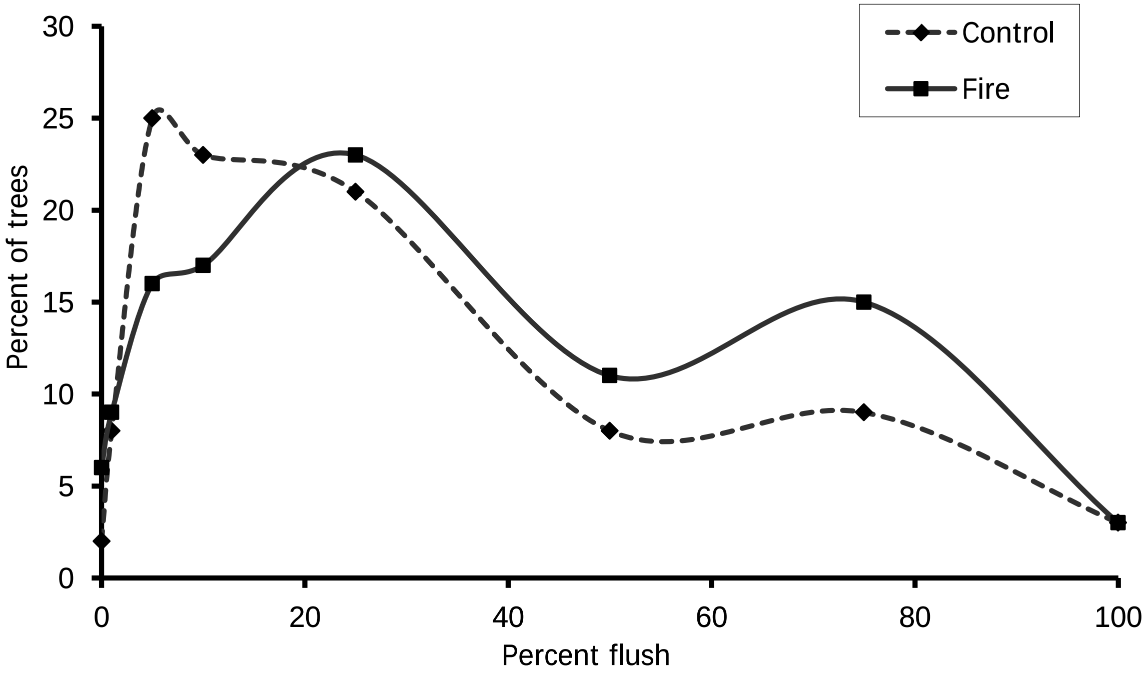

Figure 29.2. The prevalence of trees displaying foliage flush in burned and unburned areas at Puʽu Loa on Mauna Kea, Hawaiʽi.

Discussion

Unlike a prescribed burn, there were no prior data on vegetation composition and structure. However, because of their proximity, and similar tree densities, we are confident that the control plots were an adequate representation of the land before it burned. It is preferable to initiate monitoring two to six weeks after the burn to accurately quantify the degree of burned and scorched vegetation (Brown *et al*. 1982). However, we were primarily interested in the effect of fire on māmane regeneration, which was more apparent nine months later. Alien grass species were more common in burned plots than they were in the forest reserve control plots (U.S. Geological Survey unpublished data), suggesting that the likelihood of subsequent fires increases once an area has burned. By contrast, the forest reserve harbors species that respond negatively to fire, as fire is rare in this and other native communities in Hawaiʽi (Smith and Tunison 1992).

The fire burned with its highest intensity within the forest reserve, where the density of māmane and fine grass fuels (U.S. Geological Survey unpublished data) were higher. Grazing by cattle reduced the grass biomass in the pasture, which resulted in a short sward and lower fire intensity. Although results are suggestive, many other factors must be accounted for including the microclimate associated with each tree (Freifelder *et al*. 1998) and weather conditions affecting the fire's behavior when it rekindled two weeks later and burned the forest reserve. Although two-thirds of the trees in the forest reserve were defoliated, many of these were producing suckers close to their bases. This trend was even more dramatic in the pasture, where a tenfold increase in suckers was observed in the burned area. In addition, the proportion of scorched live trees with ground suckers was double that of unburned trees in the pasture, suggesting that low intensity fire can stimulate regeneration of root suckers. Nevertheless, at high intensities, as was observed in the forest reserve, fire reduced the amount of māmane regeneration. Results from a prescribed burn in Hawai'i Volcanoes National Park (HAVO) also suggest a higher rate of root suckering following a less intense burn (R. Loh, HAVO Resources Management, personal communication). Although it is difficult to compare the two studies because of different local conditions, fire intensities, and vitality of trees, the general trends are similar.

Māmane regeneration from seeds was not observed following a controlled burn in HAVO (R. Loh personal communication), and māmane seed viability was reportedly decreased by fire (C. W. Smith, Cooperative National Park Resources Studies Unit, University of Hawai'i at Mānoa, personal communication). The observed increase in the number of saplings (presumably regenerating from seed) may be a product of reduced competition and the creation of vacant niches (Hughes and Vitousek 1993), rather than the direct effects of the fire on seed viability and germination. It is possible that the thick carpet of alien grasses in control plots prevented māmane seedling establishment by acting as a physical barrier, reducing the availability of water, or by harboring insects that consumed the seedlings. Fire may support regeneration by reducing these impediments as well as increasing nutrients in the soil. Some plants respond to fire stress by producing more flowers or leaves (Gill 1981). Māmane trees in this study showed little phenological response to fire, suggesting that they did not evolve in a community shaped by frequent fires.

Results of this survey indicate that a low intensity fire may increase the regeneration of māmane trees. Although controlled burning might promote regeneration within the derelict forest of the pasture, burning will encourage the spread of fire-promoting grasses, which will increase the frequency and intensity of fire. As tree density increases, however, grass density may decrease (Thaxton and Jacobi 2009), and a succession of species may follow due to changes in microclimate around the trees. In time, species composition and the increase in moisture due to fog drip may reduce fire potential. Our limited data should not be used to justify controlled burning to speed māmane regeneration within the forest reserve. Although it is possible that māmane regeneration will increase, other native species (e.g., pūkiawe and *Deschampsia nubigena*) respond poorly to fire (Tunison *et al*. 1993). In addition, it is important to reduce the risk of intense, large fires and the spread of alien weeds. After a cycle of fire and alien weeds starts, the outcome is unknown. In the pasture, on the other hand, where few native species exist and māmane regeneration is poor, fire may be beneficial. Instead, planting native species and controlling aggressive alien weeds are more likely to be effective in restoring degraded forest.

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SECTION V: PREDATOR ECOLOGY AND MANAGEMENT

Preface

Introduced predators are a longstanding threat to Hawaiian birds, but before our work little was known about their ecology in the dry, subalpine māmane woodland of Mauna Kea, their level of threat to palila, or methods for their control. Many of our research results have been published elsewhere, but we include all our work here for completeness and convenience. We tested radio-telemetry techniques to develop skills in tracking feral cats, mongooses, and rats and to determine activity patterns of these animals, as described in Chapter 30. We also applied these techniques to investigate cat home range occupancy and movement patterns (see Chapter 31). Whereas most other diet studies rely on fecal samples to study diet, we identified food items in cat and mongoose stomachs to understand their roles as bird predators, as explained in Chapter 32. We also assessed the abundance and distribution of rats and mice, finding that rats were relatively uncommon compared to wetter forests (see Chapter 33).

Applying our new knowledge of predator ecology to understanding the impacts of predators on palila and other forest birds, we developed techniques for identifying predator species based on clues found on bird carcasses or at nests (see Chapter 34). In Chapter 35, we evaluate the extent of predation attributable to cats, mongooses, and rats at the failed nests of palila and other species. Culminating our predator research is our refinement of control methods. As we discuss in Chapter 36, trapping can be an effective way of reducing cat threats, and poison baits can be effective against mongooses and rats, although it can be challenging to maintain adequate bait when mice are abundant.

Chapter 30. Techniques for Determining Predator Activity Patterns. Daniel M. Goltz, Christopher Murray, Paul C. Banko

Chapter 31. Feral Cat Home Range and Movements. Daniel M. Goltz, Steven C. Hess, Kevin W. Brinck, Paul C. Banko, Raymond M. Danner

Chapter 32. Feral Cat and Mongoose Diet. Daniel M. Goltz, Daniel Nelson, Steven C. Hess, Paul C. Banko

Chapter 33. Rodent Survey. Chris Farmer, Daniel M. Goltz, Raymond M. Danner, Kevin W. Brinck, Steven C. Hess, Paul C. Banko

Chapter 34. Forensic Techniques for Predator Identification. Daniel M. Goltz, Paul C. Banko

Chapter 35. Impact of Predators at Bird Nests. Daniel M. Goltz, Paul C. Banko

Chapter 36. Predator Management. Daniel M. Goltz, Raymond M. Danner, Steven C. Hess, Chris Farmer, Kevin W. Brinck, Paul C. Banko

30 TECHNIQUES FOR DETERMINING PREDATOR ACTIVITY PATTERNS

Daniel M. Goltz, Christopher Murray, Paul C. Banko

Introduction

Protecting the endangered palila (*Loxioides bailleui*) from introduced mammalian predators is an important goal for their recovery (U.S. Fish and Wildlife Service 2006, Banko *et al.* 2009). We developed techniques for studying the movements, home range, and behavior of feral cats (*Felis catus*), rats (*Rattus rattus*), and mongooses (*Herpestes auropunctatus*) to facilitate control measures within Palila Critical Habitat (PCH). Feral cats were captured and radio-collared to better understand their ecology and movement patterns. We radio-collared and tracked rats to determine the spacing interval for toxic bait stations (see Chapter 36: Predator Management) and to assess the threat they pose to roosting and nesting birds. We tracked mongooses to gain information on their basic ecology in subalpine Mauna Kea, where little is known about their ecology, behavior, and the degree of threat to palila.

Methods

As a pilot study to determine the feasibility of radio-tracking mongooses, we captured (cage trap) and radio-collared an adult female mongoose with a Holohil Systems Ltd. PD-2C radio transmitter (164.432 MHz) on 19 August 1998. In 1999, we fitted Holohil model RI-2Csp transmitters to two mongooses and Holohil Systems Ltd. model MI-2 radio transmitters to five cats during 13–16 July. All cats and mongooses were anesthetized with methoxyfluorane before we attached the radio-collars. The animals were allowed to recover in the trap and then were released. In September 1999, we began intensive ground radio tracking of all these animals to determine their daily movements and activity patterns.

Feral cats are difficult to observe; therefore, we calibrated 35–37 g Holohil Systems Ltd. Model MI-2 radio transmitters with AOR AR8200 digital receivers to determine location accuracy during close-range tracking. We simulated cat behavior by handling transmitter collars both in motion and motionless at <0.5 m height through vegetation. Observers that did not know the true location of transmitters monitored the receiver’s LCD signal meter and achieved approximately 50-m accuracy. We maintained this distance during tracking to avoid disturbing the subjects.

To assess daily activity in rats, Japanese basket traps were baited with fresh coconut and placed in areas of suspected rat activity on the western slope of Mauna Kea. Three black rats were captured near 2,134 m elevation during 11–12 March 1998. Rats were transferred into a plastic bag containing cotton balls dipped in methoxyfluorane and anesthetized. Rats were then fitted with Holohil Systems Ltd. model PD-2C radio transmitters, returned to the basket traps, and allowed to recover from anesthesia. Following recovery, rats were released at the capture site. Rats were radio-tracked, and their locations were logged using a GPS unit. We observed the behavior of the radio-collared rats at night with night-vision goggles. We also located and described den sites.

Results

Mongoose 164.432 (captured and radio-tagged on 19 August 1998) was radio-tracked on several occasions, and one den site was located. During one tracking episode, the mongoose moved >1 km within a five-hour period. The mongoose appeared wary in the presence of humans and quickly moved out of sight. We did not collect a sufficient number of locations to allow a statistical analysis of home range size, but the limited data suggest a home range of >1 km^2. This animal was difficult to radio-track because it was fitted with a radio-transmitter that was designed for use on rats. The antenna on this model (Holohil model PD-2C) looped around the animal's neck to form the collar before exiting dorsally along the animal's back. When the transmitter was fitted to the mongoose, the protruding antenna length was very short (<5 cm) due to the larger circumference of the mongoose's neck. The result was decreased telemetry range. In 1999, we switched to radio-transmitters (Holohil model RI-2Csp) which had a longer antenna and produced a stronger signal.

Mongooses were active mainly during daylight hours, beginning at 0600–0800 hours and ceasing by 2200 hours (*n* = 67 observations, 2 mongooses). Activity decreased slightly during 1400–1600 hours (Figure 30.1).

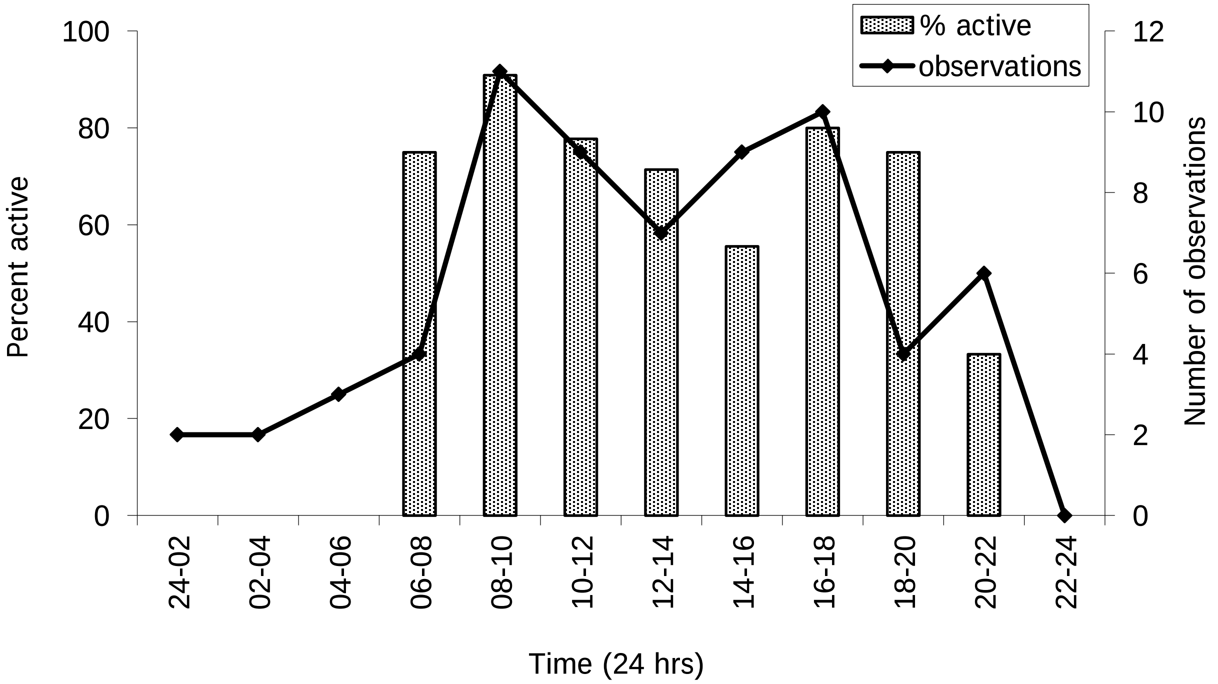

Figure 30.1. Mongoose (*n* = 67 observations, 2 mongooses) activity patterns on Mauna Kea, Hawai'i, 1999.

Feral cat activity (*n* = 293 observations, 5 cats) peaked during 2000–2200 hours but was low during the rest of the night, especially during 0400–0600 hours (Figure 30.2). Daytime activity levels declined gradually from early morning to noon before increasing to mid-afternoon.

Rat 1 (164.357 MHz), a female, was tracked for 12 weeks until the battery expired. She was re-trapped seven weeks later (6 August 1998) and fitted with a new transmitter (164.469 MHz). Rat 2 (164.243 MHz), a male, was tracked and observed for eight weeks before his transmitter fell off. Based on 16 nights of observation during 23 March–27 May 1998, both Rat 1 and Rat 2 were active primarily from sunset to 0300 hours. They spent most of their time foraging on naio (*Myoporum sandwicense*) fruit in the upper canopy of trees. They also possibly ate insects and other vegetation while in the trees. We tried to document rat behavior in the presence of a

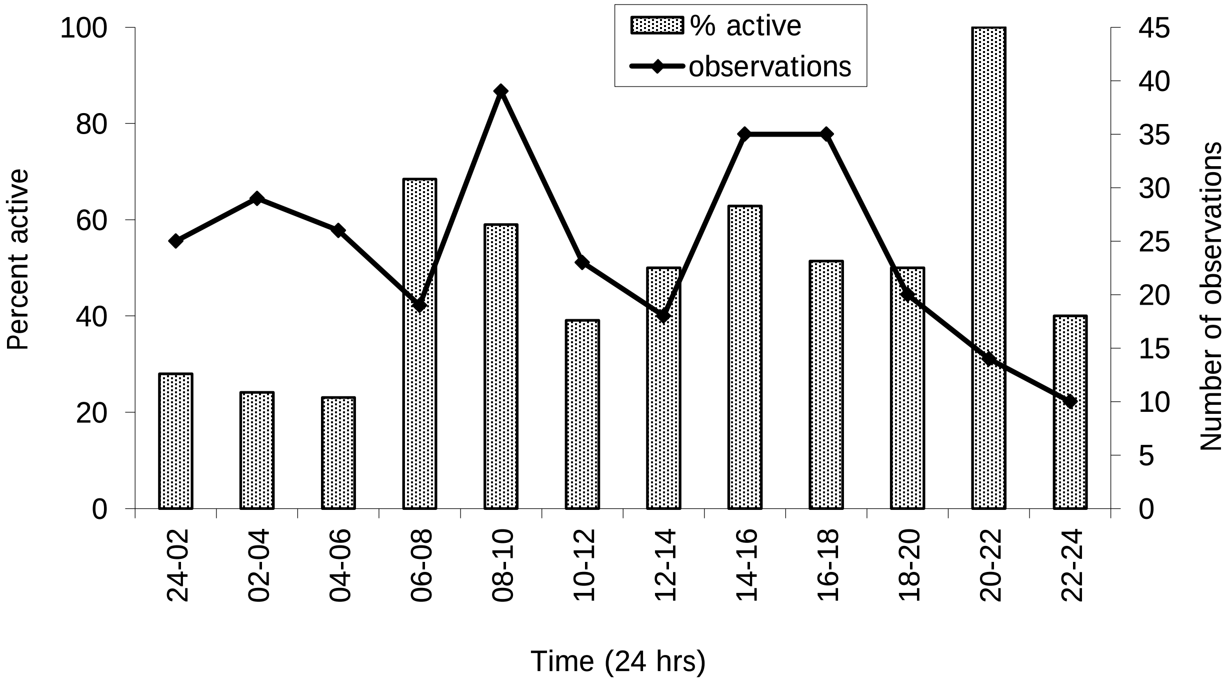

Figure 30.2. Feral cat (*n* = 293 observations, 5 cats) activity patterns on Mauna Kea, Hawaiʽi, 1999.

roosting bird, but no birds were encountered. We located one rat den in a cavity underneath a pile of lava rocks and five rat dens in trees. Three of the tree dens were in naio, and two were in māmane (*Sophora chrysophylla*). The entrance to one tree den opened at ground level, and the entrances to the other four dens ranged from 1.5 to 3.6 m above ground. During the life of its transmitter, Rat 1 occupied a home range of 1,179 m^2 (adaptive Kernel 95%, Program Calhome; Kie *et al*. 1996). When this rat was re-tagged on 6 August 1998, she had moved to a new territory. Her new home range encompassed about 650 m^2 and was located approximately 2,500 m upslope of the previous den. Rat 2 occupied a home range of 2,772 m^2.

The transmitter on Rat 3 failed less than one week after attachment, and no useable data were collected. Rat 3 was later trapped in a snap trap, and the transmitter showed evidence of being gnawed.

Discussion

The pronounced diurnal activity pattern that we found in mongooses in subalpine Mauna Kea confirms the findings of other studies (Tomich 1969, Keith *et al*. 1990). The mongoose (164.432 MHz) that we tracked in 1998 occupied a large home range (at least 1 km^2), also consistent with home range sizes reported by Tomich (1969) and Keith *et al*. (1990). Much smaller home ranges (1.4–3.6 ha) have been reported in areas of higher population densities (Hays and Conant 2003, 2007).

We also found feral cats to be strongly diurnal, contrary to our expectations. Further evidence of their diurnal predatory activity was documented at palila nests during the 1999 breeding season (Laut *et al.* 2003). The sharp peak in cat activity at 2000–2200 hours presumably reflects a favorable time to forage for rats and roosting birds. The period of lowest cat activity (0400–0600 hours) coincides with the lowest diurnal temperatures at the study site (Juvik *et al.* 1993). Radio signals often became weak or non-receivable during this period, suggesting that cats may have been entering dens or sheltered areas to avoid colder temperatures.

Our study demonstrates the effectiveness of radio telemetry in determining the home range size and behavior of feral cats, rats, and mongooses in PCH. Our results and additional ecological studies will be useful in developing management strategies to control predators in PCH.

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31 FERAL CAT HOME RANGE AND MOVEMENTS

Daniel M. Goltz, Steven C. Hess, Kevin W. Brinck, Paul C. Banko, Raymond M. Danner

Introduction

Feral cats (*Felis catus*) became abundant in forests of the Hawaiian Islands soon after their introduction in the late 1700s (Rothschild 1893, Perkins 1903, King 1984). They were later reported to be notorious predators of birds that contributed to the decline and extinction of some Hawaiian species (Perkins 1903, Berger 1981, Ralph and van Riper 1985, Stone 1985, Snetsinger *et al.* 1994, Lindsey *et al.* 2009). In Hawai'i, cats are currently important predators of terrestrial birds that nest near the ground (Kowalsky *et al.* 2002) and in trees (Hess *et al.* 2004). Cats are also important predators of colonial seabirds (Smith *et al.* 2002). Feral cats range throughout the Hawaiian Islands from high-density colonies near coastal areas where pets are frequently abandoned and fed by people (Winter 2003) to remote, low-density populations in montane forests and subalpine areas of Maui (Simons 1983) and Hawai'i Island (Hu *et al.* 2001). Despite the long history of feral cats in Hawai'i, there has been little research about their spatial arrangement or basic ecological organization, such as home range and movements.

Several studies have documented home range and movements in the Pacific region where introduced cats have established feral populations. Fitzgerald and Karl (1986) reported linear home ranges in the steep Orongorongo Valley of New Zealand. Konecny (1987) found the home ranges of male cats to be larger than those of females in the Galápagos Islands; nevertheless, Norbury *et al.* (1998) found no difference in home range size between sexes for feral cats living in dry tussock grassland in New Zealand. Edwards *et al.* (2001) documented the largest home ranges (2,210.5 ha) in semiarid woodland of central Australia. The only study of feral cat home ranges in Hawai'i was from a wet montane forest on windward Mauna Kea, at Hakalau Forest National Wildlife Refuge (Hakalau), Hawai'i Island (Smucker *et al.* 2000). These studies have contributed to the basic knowledge of the species, but have also provided information for better management of non-native predators and conservation of native fauna (Fitzgerald and Karl 1986).

The distribution and abundance of feral cats may be controlled by a number of factors including territorial behavior, social interactions, or food resources. Marked differences among individuals may exist in landscape use patterns due to foraging, mate-seeking, denning, and rearing behaviors. The spatial arrangement of feral cats can be used to gauge the timing and spacing distance of control units (e.g., traps or poisoned baits) to understand the epidemiology of diseases and to delineate the total area over which to remove resident animals and buffer against immigration (Veitch 1985, Norbury *et al.* 1998, Short *et al.* 1997, Edwards *et al.* 2001). The objectives of our study were to determine home range, territoriality, and daily movement rates of feral cats in the dry subalpine woodland of Mauna Kea, Hawai'i. This area includes the critical habitat of the palila (*Loxioides bailleui*), an endangered Hawaiian honeycreeper whose population has been declining sharply since 2003 (Banko *et al.* 2013). Feral cats prey upon palila (Banko *et al.* 2009), and knowledge of cat ecology is needed to improve control methods.

Methods

Our study area was located in subalpine woodland on Hawai'i Island on the western slope of Mauna Kea (19°49'N, 155°36'W), a dormant volcano. Subalpine woodland occurs between 1,750 and 3,000 m elevation, where tree canopy cover is sparse and interspersed with shrubs and larger areas of shrublands. Dominant trees include māmane (*Sophora chrysophylla*) and naio (*Myoporum sandwicense*) and extensive shrublands are dominated by pūkiawe (*Leptecophylla tameiameiae*), and ʽaʽaliʽi (*Dodonaea viscosa*). The semi-arid aspect of subalpine woodland is due to severely drained volcanic substrates and rain shadow effects. Rainfall averaged 511 mm and temperature averaged 11.1 ± 1.5°C annually (Juvik *et al.* 1993). There are no natural sources of perennial standing water in the study area.

Feral cats are difficult to observe; therefore, we calibrated 35–37 g Holohil Systems Ltd. model MI-2 radio transmitters with AOR AR8200 digital receivers to determine location accuracy during close-range tracking. We simulated cat behavior by handling transmitter collars both in motion and motionless at less than 0.5 m height through vegetation. Observers that did not know the true location of transmitters monitored the receiver's LCD signal meter and achieved approximately 50-m accuracy. We maintained this distance during tracking to avoid disturbing the subjects.

We captured seven male and three female cats, anesthetized them with methoxyfluorane, and fitted them with transmitters during 1999–2000. Cats were allowed to fully recover in traps and were not tracked for at least one day after release. Six male cats were fitted with transmitters in July 1999. One cat (M-4) was opportunistically recaptured after 14 months and fitted with a new transmitter to extend data collection. Three females and one additional male cat were fitted with transmitters in September 2000. The weight of males ranged from 2.4–3.65 kg (mean = 2.99 kg) while females ranged from 1.75–2.2 kg (mean = 1.86 kg). All cats were adults, based on dentition. We recorded at least three locations per cat per day with Garmin GPS 12 receivers. Cats were periodically tracked on consecutive days to determine daily movements. Data collection ended in February 2002.

To investigate the temporal autocorrelation of observations, we calculated t2/r2 statistics for a range of minimum times between observations (Swihart and Slade 1985, 1986). A minimum separation of 2.85 days was needed to achieve quasi-independent observations. We excluded data points that were taken ≤2.85 days after the first observation and points that were ≤2.85 days after subsequent observations. We calculated 95%, 50%, and 25% fixed kernel (Worton 1995) home ranges using the animal movement extension (Hooge and Eichenlaub 1997) for ArcView GIS (ESRI 1999). We used least squares cross-validation to estimate a kernel smoothing parameter for each cat and used the median value (378 m) for all cats to produce the final home range estimate as recommended by Seaman and Powell (1996). We then examined the effect of reduced sample size on kernel home range estimates with 1000 bootstrap minimum convex polygons (MCP) from the remaining locations using the animal movement extension (Hooge and Eichenlaub 1997). We plotted MCP area against sample size to determine if sufficient observations existed to stabilize MCP area. We compared log-transformed 95% and 25% kernel home range estimates between sexes with t-tests.

To estimate the daily movements of feral cats, we calculated both the simple mean rate of speed between all successive observations per day and the mean rate of speed weighted by time between all successive observations per day. In the weighted mean estimate of daily movements, greater periods of time are proportionally more important than shorter periods and therefore reflect a more accurate rate. We compared the simple mean rate of speed (meters/day) of males and females between all successive observations with t-tests.

Results

Fixed kernel home range estimates were determined to be reliable for seven of the ten subjects through bootstrap minimum convex polygon analysis (see also Goltz *et al.* 2008). Estimates of 95% fixed kernel home ranges for these seven cats ranged between 610 and 2,050 ha and averaged 1,418 ha for males and 772 ha for females (Table 31.1). Excluding points to achieve quasi-independence resulted in an average increase of 28% in the 50% core activity areas, although overall 95% kernel home ranges were smaller when compared to analyses using all observations. Log-transformed 95% kernel home ranges for males were significantly larger than those of females (Equal variance 2-sample t-test; df = 5, t = -3.20, P = 0.024), but 25% kernel home ranges of females were larger than those of males (df = 5, t = 3.53, P = 0.017; Figures 31.1 and 31.2).

Table 31.1. Kernel home range estimates of feral cats (*Felis catus*) on Mauna Kea, Hawai'i, 1999–2002. Non-independent observations were eliminated based on 2.85 days between quasi-independent observations. Home range was calculated by the median least square cross validation H (LSCV H) value of 378.

		Observations			Home range (ha)		
ID	Days to quasi-independence	*n* (all)	*n* (2.85)	LSCV H	95%	50%	25%
M-1	0.25	26	9†	600	637	55	24
M-1	0.05	30	8†	298	428	60	26
M-2	0.04	66	29	416	1,167	98	37
M-3	4.00	70	18†	399	739	80	29
M-4	6.65	179	43	542	2,050	152	29
M-5	0.05	112	46	358	1,279	116	32
M-6	1.00	19	6†	386	432	80	24
M-7	8.00	73	30	428	1,176	84	32
F-1	4.95	135	31	291	875	169	61
F-2	1.70	130	27	292	831	202	58
F-3	6.90	183	44	195	610	100	39

†Sample size not sufficient for reliable kernel home range estimates

Cat M-1 exhibited sequentially clustered observations separated by 14.8 km and was therefore treated as having two separate home ranges, although sample size was insufficient for reliable kernel estimates for either home range. He initially ranged on the western slope for five months before shifting to the southern slope (Figure 31.1). Cat M-4 shifted his fall/winter range downslope several kilometers over the course of one year. Cat M-7 periodically traveled from the western slope to the northeastern slope and back, covering at least 25 km in two days. Cat M-3 traveled between the western and northern slopes of Mauna Kea, making a 45-km roundtrip during a two-week period, but there were insufficient samples for generating a reliable kernel estimate. None of the female cats shifted their ranges during the study. Cat F-3, the female with the smallest range and daily movements, raised two litters of kittens during the study.

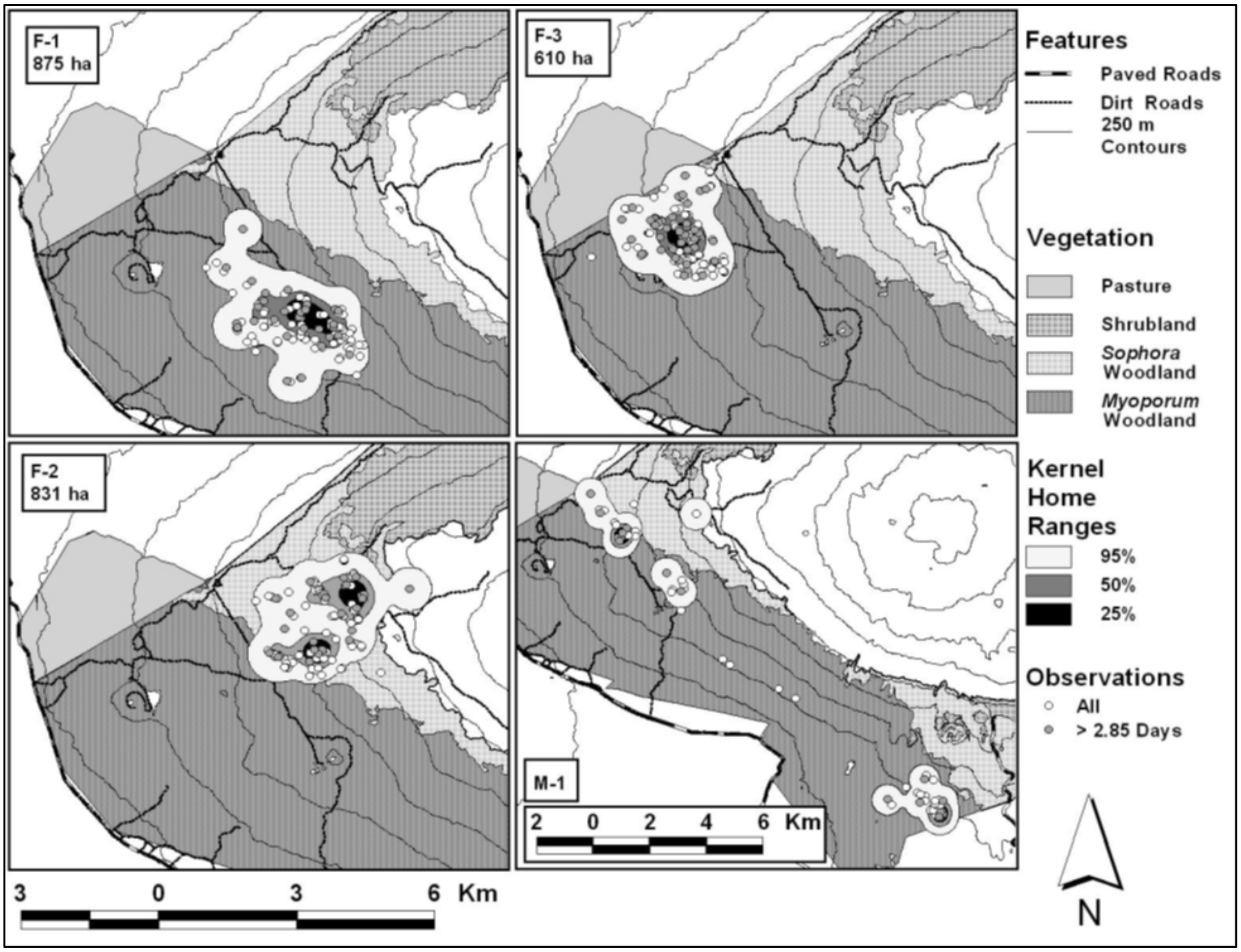

Figure 31.1. Telemetry observations and fixed kernel home ranges of one male and three female feral cats on the western slope of Mauna Kea, Hawai'i, 1998–2001. Non-independent observations were eliminated based on an estimated average of 2.85 days to quasi-independence.

Home ranges of male cats overlapped extensively, whereas home ranges of females overlapped very little (Figures 31.3 and 31.4). Two male cats with overlapping ranges were separated on average by 1.4 km on the 10 days when both cats were tracked simultaneously. They were once separated by 60 m within a span of 30 minutes, and again by 320 m in a 75-minute span.

Weighted mean daily movements of cats ranged from 35–157 m/day with an overall average of 81.8 m/day (Table 31.2). Mean daily movement rates between sexes overlapped widely (females = 62 m ± 3.3 [SE]; males = 90 m ± 17.2) and did not differ significantly (unequal variance 2-sample t-test; df = 6, $t = -2.08$, $P = 0.083$).

Discussion

Mean home ranges of feral cats on Mauna Kea were the largest reported among seven other studies from the Pacific region for females (mean = 79.9% larger) and the second largest for males (mean = 56.1% larger; Table 31.3). We found that home ranges of male feral cats on

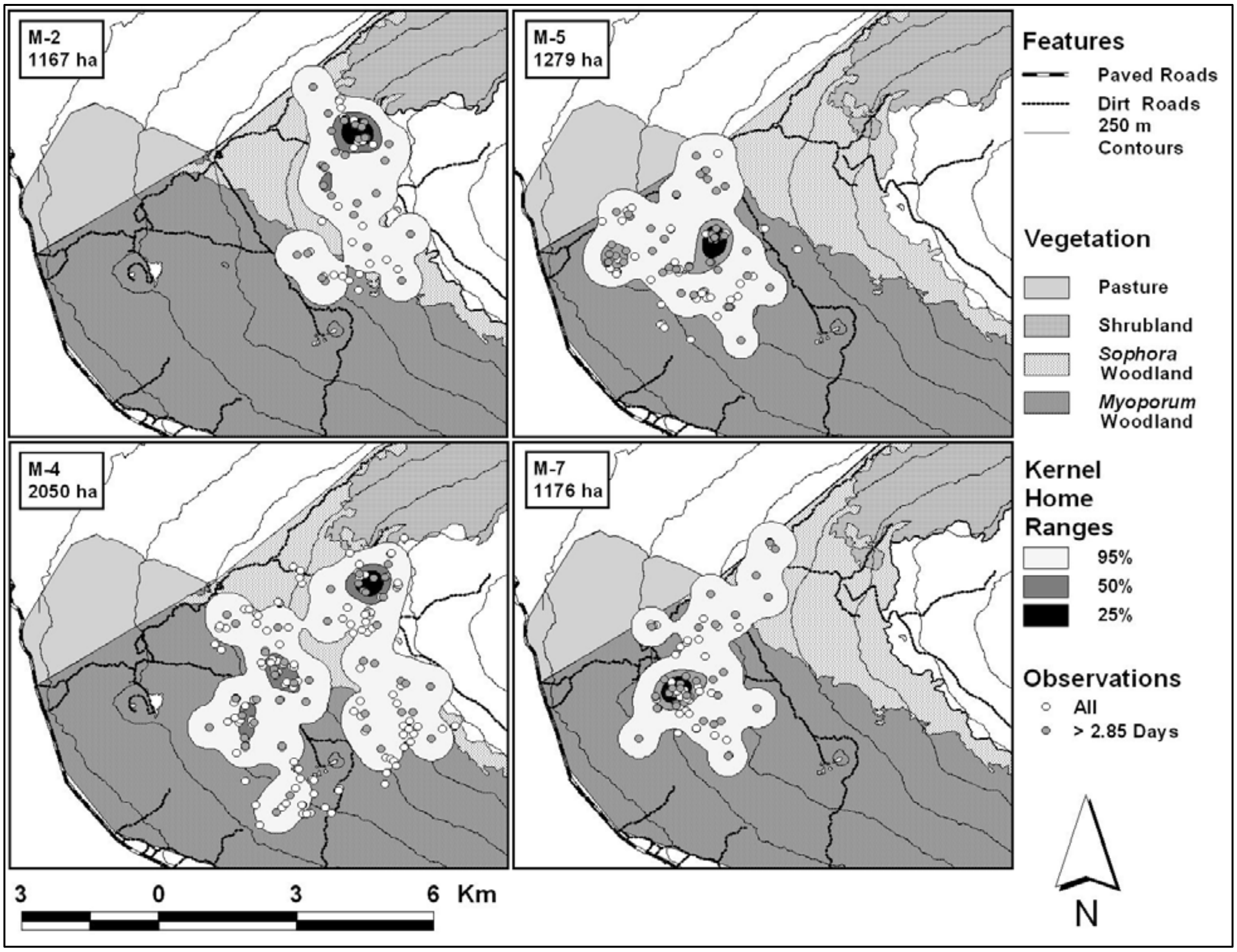

Figure 31.2. Telemetry observations and fixed kernel home ranges of male feral cats on the western slope of Mauna Kea, Hawai'i, 1998–2001. Non-independent observations were eliminated based on an estimated average of 2.85 days to quasi-independence.

Mauna Kea were 60% larger and female home ranges were 71% larger than those reported from Hakalau, which is approximately 25 km in distance from our study site and consists mainly of montane wet forest and former pasture habitat that is being restored to forest (Smucker *et al.* 2000). Moreover, home ranges (log-transformed) of males were also significantly larger than those of females throughout the Pacific region (df = 12, t = -2.25, P = 0.044).

Although Jones and Coman (1982), Konecny (1987), and Norbury *et al.* (1998) used minimum convex polygon analyses, the larger home ranges on Mauna Kea represent more than a methodological discrepancy. Home ranges were comparably sized in the environment most similar to Mauna Kea; semiarid woodland of the Northern Territory of Australia (Edwards *et al.* 2001). Edwards *et al.* (2001) and Smucker *et al.* (2000) also based their estimates on kernel methodology, but our estimates of overall home ranges may be comparatively smaller in area because we eliminated non-independent points. No other studies explicitly accounted for the independence of locations; nevertheless, Norbury *et al.* (1998) examined the effect of sample size on home range estimates and found that home range size began to stabilize after about

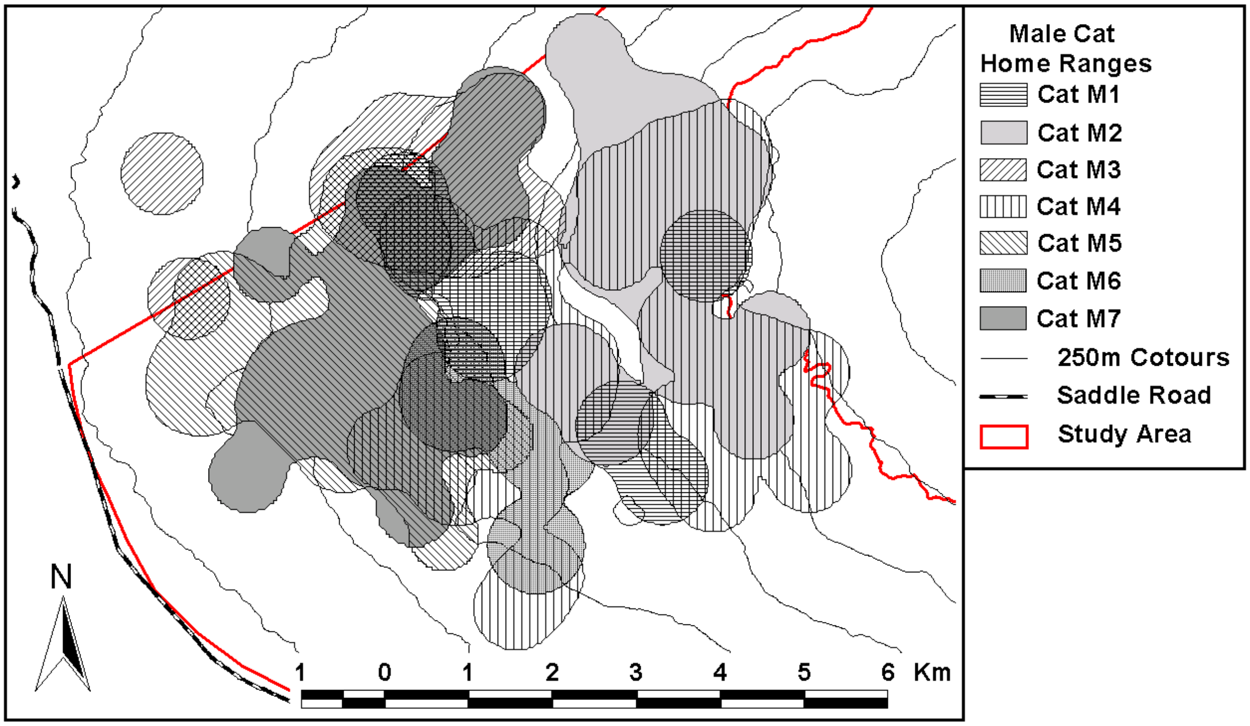

Figure 31.3. Overlap of 95% kernel home ranges for seven male feral cats on Mauna Kea, Hawai'i, 1999–2000.

10 locations. We could not calculate reliable home range estimates from animals with ≤18 locations. Only two of five cats in the Smucker *et al.* (2000) study were tracked to >18 locations; therefore, sample sizes may have been inadequate, resulting in underestimation of true home range size.

We found some evidence that the spatial arrangement and low density of feral cats on Mauna Kea was tied to social organization. There were strong differences between sexes in home range size, which we attributed primarily to mate-seeking behavior in males and denning behavior in females. Although females on Mauna Kea occupied large areas relative to other study locations, their overall mean home ranges were only 54% as large as males, but their core activity areas were larger than those of males indicating they may use smaller areas more intensively while males use larger areas more extensively. Konecny (1987) also found differences between sexes and that female cats with kittens occupied extremely restricted ranges. Norbury *et al.* (1998) and Molsher *et al.* (2005), on the other hand, found no difference between sexes in home range for cats in dry tussock grassland in New Zealand and central-western New South Wales, Australia, respectively. The relative sizes of male and female home ranges may differ among these study environments due to the breeding frequency of females and the mate-seeking and foraging behaviors of males in different habitats.

Although we did not find other reports of daily movements in the literature, we documented average daily movements of about 82 m/day and some much greater maximum movements. Because mean daily movements on Mauna Kea did not differ between sexes, males apparently did not always return to the same location on a daily basis, whereas females may have been

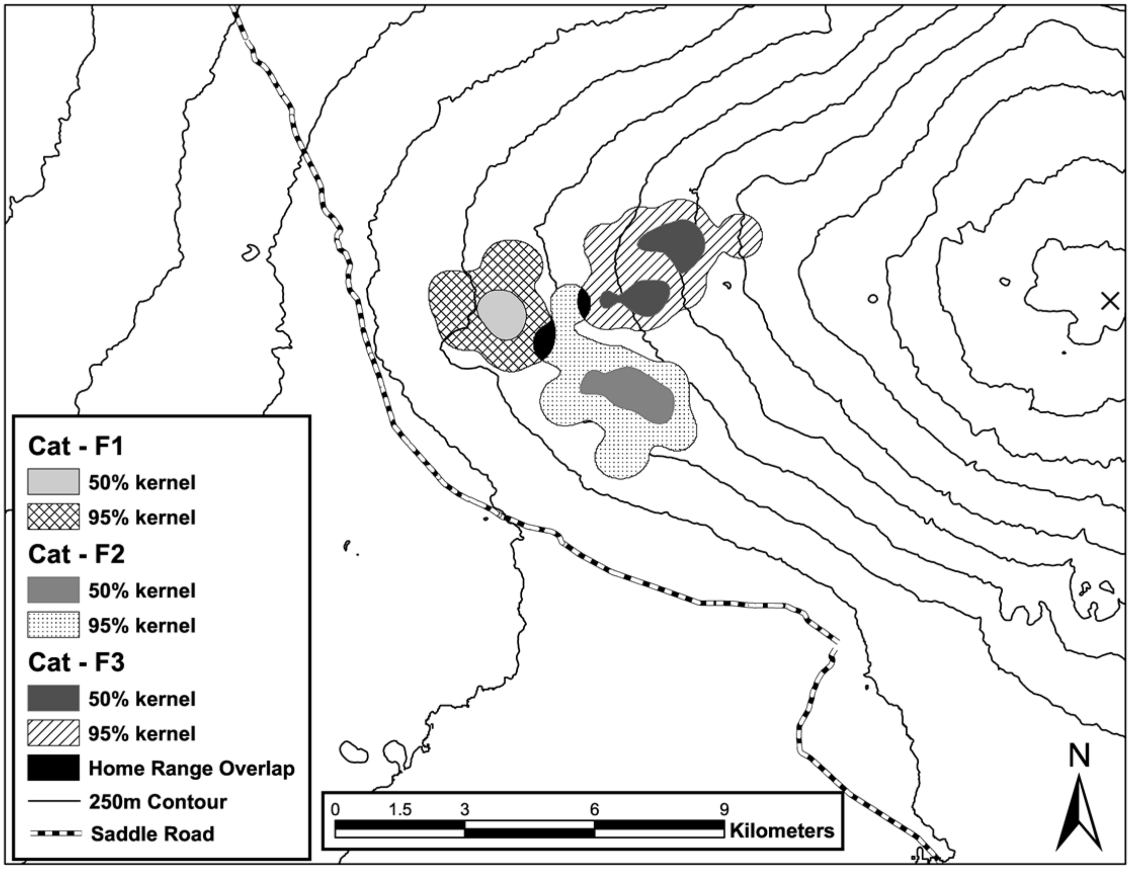

Figure 31.4. Home ranges of three female feral cats on Mauna Kea, Hawai'i, 1999–2001, showing no overlap of 50% kernel estimates and slight overlap of 95% kernel estimates.

Table 31.2. Simple and weighted mean daily movements of feral cats on Mauna Kea, Hawai'i, 1999–2002.

ID	*n*	Simple mean (m/day)	Weighted mean (m/day)
M-1	56	4,521.5	123.5
M-2	63	6,014.3	157.4
M-3	70	4,901.4	75.9
M-4	179	153.7	84.5
M-5	112	109.8	35.1
M-6	19	90.9	62.4
M-7	73	124.9	92.1
F-1	135	108.6	64.0
F-2	130	112.4	66.8
F-3	183	183.7	55.8

Table 31.3. Comparison of home range estimates from the western slope of Mauna Kea, Hawai'i, with seven other published studies from the Pacific region. Percent by which Mauna Kea (MK) cat home range was greater compared to another study area = $(1 - (HR_{\text{study } x}/HR_{\text{Mauna Kea}})) \times 100$.

	Home range size (ha)		Percent by which MK cat home range was greater	
Habitat and location	Female	Male	Female	Male
Subalpine woodland, Mauna Kea, Hawai'i	772	1,418	–	–
Wet montane forest, Hakalau, Hawai'i[a]	223	574	71.1%	59.5%
Galápagos Islands[b]	82	304	89.4%	78.6%
Orongorongo Valley, North Island, NZ[c]	80	140	89.6%	90.1%
Dry tussock grassland, South Island, NZ[d]	225	225	70.9%	84.1%
Victorian Mallee, south-eastern Australia[e]	170	620	78.0%	56.3%
Open forest, New South Wales, Australia[f]	140	288	81.9%	79.7%
Semiarid woodland, central Australia[g]	–	2211	–	-55.9%
Mean	241.7	722.4	80.1%	56.1%

[a]Smucker *et al.* 2000, [b]Konecny 1987, [c]Fitzgerald and Karl 1986, [d]Norbury *et al.* 1998, [e]Jones and Coman 1982, [f]Molsher *et al.* 2005, [g]Edwards *et al.* 2000

tied to a central location, such as a den. It is unlikely that all dens were permanent, but some lava tubes were used more than once, sometimes by different cats. Lava tube dens were probably used repeatedly since they provide good shelter. Fitzgerald and Karl (1986) reported that feral cats did not have permanent dens, but could be found resting in any part of their home range. Jones and Coman (1982) found that cats favored areas within their home ranges that provided good shelter.

In studies where food sources were abundant and concentrated, a large degree of spatial overlap occurred among male cat home ranges, but activity centers were discrete and encounters with conspecifics were rare (Konecny 1987, Short *et al.* 1997). Smucker *et al.* (2000) reported that male home ranges had minimal overlap in montane forest at Hakalau. In subalpine Mauna Kea, however, male cat home ranges overlapped extensively, including the 25% core activity areas of M-2 and M-4. There was no apparent seasonal pattern to home range overlap; however, the range of M-4 extended to lower elevation primarily during March–August 2001, and subsequently returned to higher elevation. Evidence for territorial encounters between males on Mauna Kea comes from the prevalence of feline immunodeficiency virus (FIV), which is primarily transmitted by biting and scratching (Yamamoto *et al.* 1988). While 17% of 39 males from Mauna Kea tested positive for FIV, all 29 females were negative (Danner *et al.* 2007). Overall female home ranges on Mauna Kea overlapped only slightly, and core activity areas did not overlap.

Feral cats are wide-ranging predators with negative effects on the native fauna throughout the Pacific region (Dickman 1996). Hansen *et al.* (2007) estimated that 17.6% of cats per generation on Mauna Loa, primarily males, had migrated >53 km from Mauna Kea. There is evidence that feral cats in Hawai'i prey on endangered forest birds (Laut *et al.* 2003, Hess *et al.* 2004) as well as nesting seabirds (Smith *et al.* 2002, Hess *et al.* 2007). Male cats tend to be more wide-ranging than females and may therefore encounter more endangered birds while foraging. For example, the mean home range of male cats on Mauna Kea represents more than 10% of the entire range (140 km^2) occupied by the palila (Scott *et al.* 1986). Because male home ranges were also nonexclusive, palila may be simultaneously exposed to predation by several different individual cats.

Trap spacing should account for minimum daily movements and differences between sexes in home range. The radius of a circular area equivalent to the home range of female feral cats on Mauna Kea is 1,568 m and males is 2,125 m. Cats may be expected to encounter traps when traps are spaced at shorter distances, but daily movements may be used to guide minimum spacing between transects during short-term (two to three days) trapping sessions. Most subjects moved >100 m per day. The implications of large home ranges in male cats is that large trapping areas are needed to confine immigration to buffer zones on the perimeter of endangered species habitat in this environment in Hawai'i.

Other considerations are also important for effective trapping programs. Short *et al.* (2002) found that feral cats that did not use rubbish dumps were more likely to be caught in concealed foot-hold traps than cage traps. No such human subsidies currently exist within the range of cats on the western slope of Mauna Kea.

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32 FERAL CAT AND MONGOOSE DIET

Daniel M. Goltz, Daniel Nelson, Raymond M. Danner, Steven C. Hess, Paul C. Banko

Introduction

Introduced, carnivorous small mammals threaten native Hawaiian bird communities, but evidence of their impacts is often difficult to gather due to their secretive behavior and generally small populations. Diet studies can provide a direct indication of the effects of predators on prey species. Feral cat (*Felis catus*) diets, especially in Hawai'i, typically include many birds and rodents (Snetsinger *et al*. 1994; Hess *et al.* 2007a, b; Lindsey *et al.* 2009). The small Indian mongoose (*Herpestes auropunctatus*) has a wide, varied diet that includes rodents, birds, insects, and vegetation (Mostello 1996). Earlier studies characterized feral cat and mongoose diets primarily through the examination of feces (Kami 1964, Snetsinger *et al*. 1994, Mostello 1996). We examined the digestive tract contents of cats and mongooses to determine the relative importance of various prey in their diets.

Methods

We collected feral cat and mongoose stomachs and intestines during seven trapping sessions (April 1998–May 2004) on the northern and western slopes of Mauna Kea and preserved them in 70% ethanol. We cut stomachs and intestines along the entire length with scissors. We attached a garden sprinkler to a hose and sprayed a continuous, gentle stream of water over the digestive tract contents. With gentle pressure from fingers, we rinsed and filtered the contents in soil sieves (U.S. Bureau of Standards size 5 and 10 mesh). We collected insects, vegetation, hair, large feathers, and large pieces of rodents and birds in the size 5 sieve. We collected small feathers, hair, seeds, and small bones in the size 10 sieve. We identified the contents with the help of a reference collection of items from Mauna Kea and various reference keys. We noted the presence of each item in the digestive tracts and identified items to the lowest taxonomic level practical. We then grouped these into categories for analyses. We calculated the frequency of occurrence as the number of digestive tracts containing a particular prey item divided by all digestive tracts of cats or mongooses.

Results

We examined the digestive tracts of 118 feral cats and 83 mongooses (Table 32.1).

Table 32.1. Date, location (slope), and number of carnivore digestive tracts collected on Mauna Kea, Hawai'i.

Session	Date	Location	Cat	Mongoose
1	30 Apr–2 Jul 1998	North	14	1
2	28 Jul–20 Aug 1998	West	13	11
3	10 Sep 1998–4 Mar 1999	North	18	8
4	15 Jun–15 Jul 1999	West	1	0
5	9 Apr–21 Jun 2002	West	20	39
6	30 Jun–13 Aug 2003	West	31	14
7	4 Nov 2003–16 May 2004	North	21	10
Total			118	83

In feral cat samples, the most common animal prey type was birds (78.8% of all samples contained birds of all taxa, “all birds;” Figure 32.1). The prevalence of Passeriformes and Galliformes birds was particularly high in cats collected on the western slope (Figure 32.2). We found many Hawaiʽi ʽamakihi (*Loxops virens*), a house finch (*Carpodacus mexicanus*), a Hawaiʽi ʽelepaio (*Chasiempis sandwichensis*), and possibly a palila (*Loxioides bailleui*) in the cat samples. We recovered aluminum leg bands from two Hawaiʽi ʽamakihi and one Hawaiʽi ʽelepaio from western slope cats. Of the cats sampled during trapping session 7, 19.4% contained eggshell fragments. Eggshell data were not collected in other sessions. Cats ate insects from the orders Coleoptera, Diptera, Lepidoptera, and Odonota.

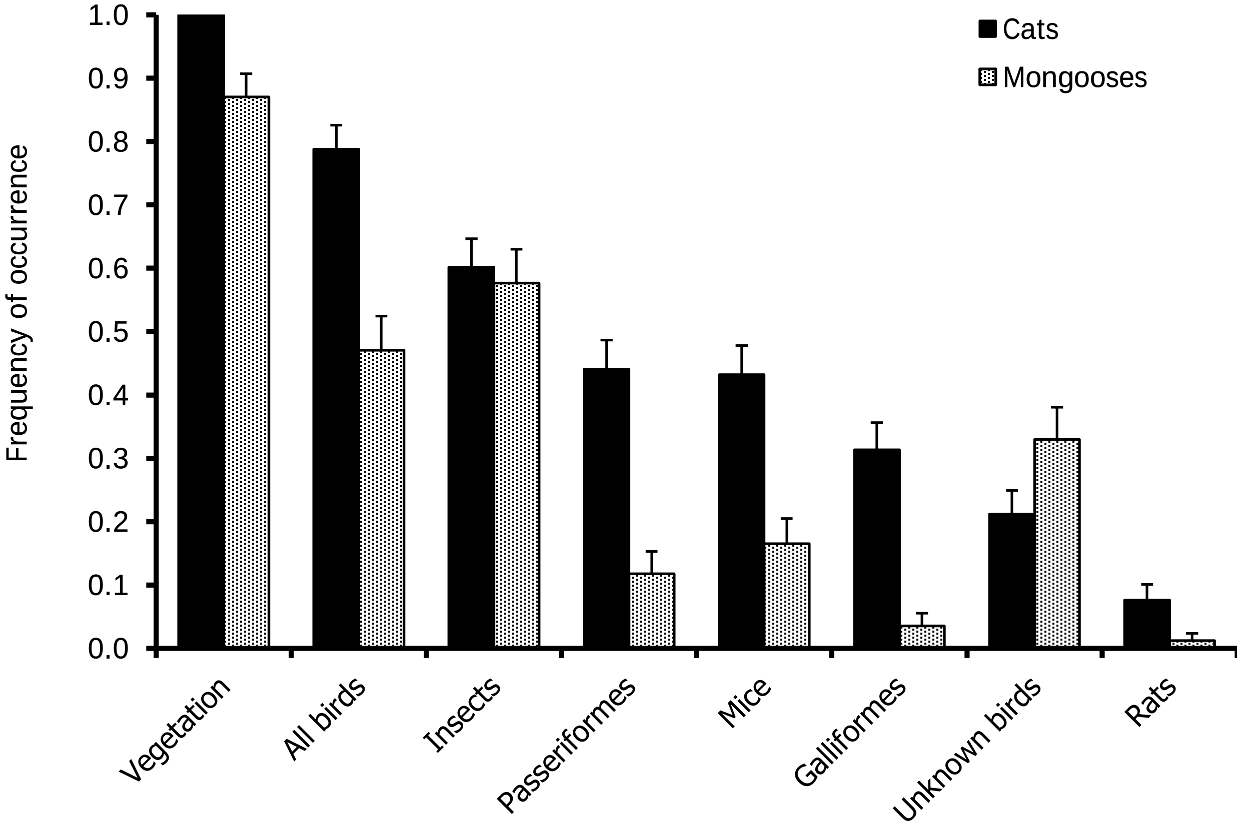

Figure 32.1. Frequency of occurrence (± SE) of prey items from cat and mongoose digestive tracts from Mauna Kea, Hawaiʽi, 1999–2004. “All birds” indicates remains of any type of bird, including Galliformes, Passeriformes, and unknown taxa “unknown birds.”

In mongoose samples, insects (57.6%) were the most common animal prey, followed by all birds (47.0%), unknown taxa of birds (32.9%), mice (16.4%), and Passeriformes (11.8%), with very few Galliformes and rats (Figure 32.1). Mongooses commonly consumed insects from the orders Diptera, Hymenoptera, and Odonota. Eggshell data were not collected for mongooses.

All feral cat and most mongoose samples contained vegetation, including various grasses, ʽāweoweo (*Chenopodium oahuense*) leaves, māmane (*Sophora chrysophylla*) leaves and seeds,

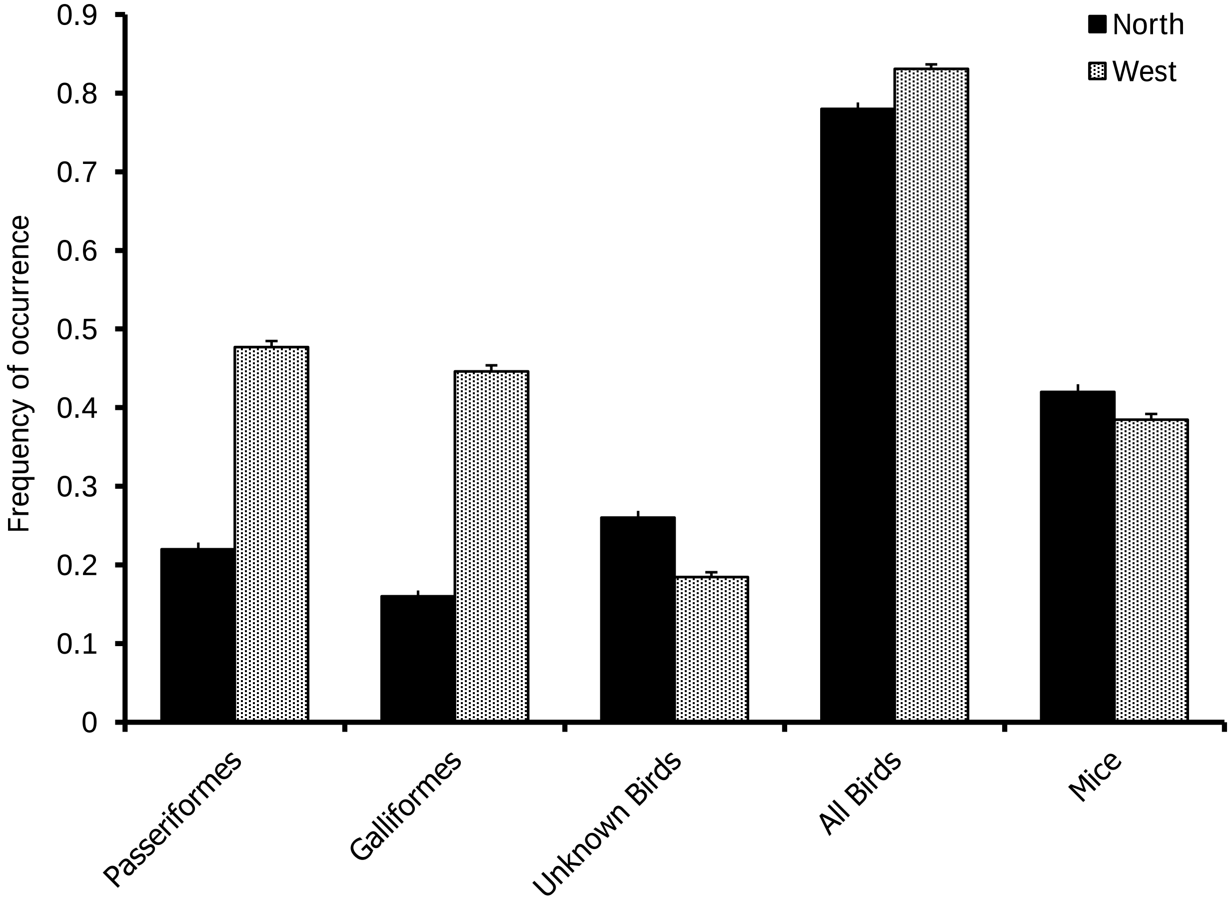

Figure 32.2. Frequency of occurrence (± SE) of major prey items from cat digestive tracts from the northern and western slopes of Mauna Kea, Hawaiʽi, 1999–2004.

and pūkiawe (*Leptecophylla tameiameiae*) leaves and berries. We have no way of knowing whether any of this material may have been ingested incidentally.

Discussion

Bird remains were frequently encountered in our cat and mongoose samples compared to other studies on Mauna Kea and elsewhere on Hawaiʽi Island (Table 32.2). For example, Hess *et al.* (2007a, b) found bird remains in <30% of cat digestive tracts collected from Mauna Loa and Kīlauea volcanoes in Hawaiʽi Volcanoes National Park. Although Snetsinger *et al.* (1994) identified bird fragments in many feral cat scats in subalpine Mauna Kea, rodents were more frequently found. Moreover, our finding of bird fragments in 47% of the mongoose samples was approximately 10 times greater than the frequency reported by Mostello (1996) and Kami (1964), who collected mongoose scats below 600 m elevation in wet habitats in the Hāmākua District of Hawaiʽi Island. Mostello (1996) reported egg shells in both cat and mongoose scat. Similar to our results, Kami (1964) reported insects in 41–80% of mongoose scats, but he found a higher incidence of rodent remains (24–72%) compared to our results. Amarasekare

Table 32.2. Frequency of occurrence of prey in digestive tracts and scats of feral cats in five studies on the western slope of Mauna Kea.

Study (sample size)	All bird	Rodent	Mouse	Rat	Insect	Eggshell
This study (*n* = 118)	0.79		0.43	0.08	0.60	–
van Riper[1] (*n* = 18)	0.39	0.39	0.33	0.06	0.11	–
Amarasekare[2] (*n* = 45)	0.12	–	0.95	0.48	0.46	0.10
Snetsinger *et al.*[3] (*n* = 87)	0.68	0.87	–	–	0.17	–
Smucker *et al.*[4] (*n* = 17)	0.53	–	0.76	0.29	0.47	–

[1] (1978), digestive tract
[2] (1994), scat
[3] (1994), scat from western and eastern Mauna Kea
[4] (2000), scat

(1994) observed rats, mice, and insects, but no birds in mongoose scats collected on the western slope of Mauna Kea.

Much of the discrepancy in reported occurrences of prey types probably arises from differences in methodology. We expect that examining stomach contents produces more identifiable remains than examining scat, in which contents pass through the entire digestive system. Still, our findings indicate exceptionally high rates of predation on birds by feral cats and mongooses. The high frequency of Galliformes and Passeriformes in feral cat digestive tracts from the western slope may be an artifact of the ability of different teams to identify the remains of prey, because the frequency of the remains of all bird taxa in western and northern slope samples was similar.

Our results highlight the prominence of birds in the diets of mongooses and especially feral cats in subalpine Mauna Kea. Reducing feral cat numbers can help protect the endangered palila.

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33 RODENT SURVEY

Chris Farmer, Daniel M. Goltz, Raymond M. Danner, Kevin W. Brinck, Steven C. Hess, Paul C. Banko

Introduction

Introduced rodents may impact native species directly through depredation or indirectly by subsidizing populations of other predators that also prey upon native species. As in many other species of rodents, the house mouse (*Mus musculus*) is known to have population irruption cycles on the Hawaiian Islands including Haleakalā, Maui (S. Anderson, Haleakalā National Park, personal communication), and Mauna Kea, Hawaiʽi, that appear to follow multiple-year precipitation cycles (Tomich 1986). The causes and consequences of population irruptions are little known. Nevertheless, given its periodic high abundance, mice may impact native arthropod abundance and consume native plant seeds, thereby reducing vegetative regeneration. Moreover, mice are key prey species for feral cats (*Felis catus*), mongooses (*Herpestes auropunctatus*), and owls (*Asio flammeus sandwichensis* and *Tyto alba*; Amarasekare 1994, Snetsinger *et al*. 1994; see Chapter 32: Feral Cat and Mongoose Diet). As prey, they help support predator populations that also prey upon native bird species, including the endangered palila (*Loxioides bailleui*). Furthermore, these predators may become abundant during rodent irruptions, resulting in greater impacts on less common, native prey species after mice again become scarce.

On Mauna Kea, mice and rats (*Rattus rattus*) climb native trees, presumably to forage on insects or fruits, where they may encounter palila and other native birds. Egg depredation by mice has not been reported in Hawaiʽi, but is known to occur in laboratory settings (King 1990). Outside Hawaiʽi, *Peromyscus* mice are major nest predators of many birds including some warbler species (Haskell 1995), giving rise to concerns that *M. musculus* also could prey on the eggs of Hawaiian forest bird species. Rats are more often implicated in nest depredation (Lindsey *et al.* 2009), but rats are not abundant on Mauna Kea (Amarasekare 1994; see Chapter 35: Impact of Predators at Bird Nests). To better understand the threats posed to palila and other native birds, we assessed rodent population trends on the western slope of Mauna Kea using biannual snap-trap monitoring. We also examined rodent habitat use patterns, morphology, age, sex ratios, and pregnancy rates during selected surveys. We determined rodent arboreal activity in a single, separate and independent trapping session.

Methods

We conducted rodent surveys for one month biannually in winter (January and February) and summer (June and July) during 2000–2005 (*n* = 10 surveys) at stations along Hawaiʻi Forest Bird Survey (HFBS) transects on the western slope of Mauna Kea, Hawaiʽi (see Introduction Figure I.2). We conducted summer 2000–winter 2003 surveys on transects 101, 122, 124, and 126 and summer 2003–winter 2005 surveys only on transects 122 and 124. We placed snap traps on 40 x 40 m vegetation plots, which were offset up to 50 m at random distances and directions from HFBS stations, between 1,811 and 3,021 m elevation (see Chapter 25: Vegetation Survey in Palila Critical Habitat). The trapping array consisted of two Victor® mouse snap traps placed 2 m apart and one Victor® rat snap trap halfway between them. This trap array was placed at the northern and southern ends of the vegetation plots, resulting in a total of six traps per station. We distributed and pre-baited the traps with shredded coconut on Thursdays or Fridays, but did not set them. On Mondays we baited and set the traps. We checked and re-set the traps, if sprung, on Tuesdays, Wednesdays, and Thursdays. On Fridays we checked, collected, and distributed these traps on the next transect. This scheme provided 4 trap-nights per trap, or 24 trap-nights (mouse and rat traps combined) per station. We calculated mouse capture rates using the number of trap-nights for both rat and mouse traps. We assumed that rats would not be caught in mouse traps, so we calculated rat capture rates using only rat trap-nights. During summer 2000–winter 2003, we trapped at 34–51 stations per transect, yielding 1,280 rat trap-nights and 3,840 mouse trap-nights per survey. The summer 2003–winter 2005 surveys yielded 600 rat and 1,800 mouse trap-nights per survey. During these three surveys, we trapped at 34–41 stations per transect. During the summer 2000 survey we placed a J. T. Eaton Peanut Butter Bait Block® at the center of the vegetation survey plots three days before setting the traps in order to detect rodents. We assumed that a single, small block of non-toxic rodent census bait would not attract rodents from outside the vegetation plot.

We corrected our number of trap-nights, or the trapping interval, to account for sprung traps, which reflects sampling effort more accurately. We used the formula developed by Beauvais and Buskirk (1999): corrected trap-nights (CTN) = (traps × interval or trap-nights) − (sprung traps × 0.5). We report the corrected trap rate here as the number of individuals/100 CTN.

In order to evaluate environmental effects on rodent abundance, we compared the capture rates from the first five surveys among habitat types: māmane (*Sophora chrysophylla*) forest, mixed māmane-naio (*Myoporum sandwicense*) forest, naio forest, and pasture (Jacobi 1989). We had detected heavy predation on ʽiliahi (*Santalum paniculatum*) seeds on the western slope near Puʽu Ahumoa, so we established an additional rodent trapping grid centered in a small grove of ʽiliahi trees with a control plot approximately 180 m away. Except for the ʽiliahi trees, the habitat around both plots consisted mainly of naio and māmane, typical of the western slope. Each plot contained 45 rat snap traps in a 40 x 40 m grid, and the traps were active from 24 March–4 April 2003 for 360 trap-nights per plot (353 CTN in the ʽiliahi plot, 349.5 CTN in the control plot).

We also examined the effect of median rainfall during the prior six months on capture rates and compared capture rates between pasture and non-pasture stations with data from summer 2000–summer 2002. We used rainfall data from Halepōhaku, Mauna Kea, for comparisons with the transect trapping data. We were unable to obtain reliable, local rainfall data for the more recent surveys. With data from summer 2002–summer 2003, we analyzed season, sex, age:season, and age:sex as categorical predictors, using a general linear model with the natural log of mouse weight as the response variable. In order to determine if mouse abundance was directly related to season, we compared capture rates from the first eight surveys between seasons (summer vs. winter). We also compared pregnancy rates and the mean number of fetuses for mice from the summer 2002–summer 2004 surveys. In winter and summer 2004, we measured the anal-genital distances of mice in order to determine if this measurement is a reliable sexing tool. Because of the extremely small sample size, we did not analyze the pregnancy rates of rats, nor the factors affecting rat weight for any of the surveys. We did not record morphological data for mice during the winter 2005 survey due to an extremely high capture rate.

We compared our census block data with the summer 2000 presence/absence snap-trap data using a paired, non-parametric binomial test for a discrete dataset of 0 (absence of mice) and 1 (presence of mice; SPSS 1.0, IBM Corp., Armonk, NY). Our paired sample was the two different survey methods at the same trap site. All data pairs with sprung traps were excluded from the test, which investigated the mean binomial probability of detecting the presence/absence of a mouse via snap-trapping compared with census blocks over 551 trap-nights.

We assessed arboreal activity of rats on the northern slope of Mauna Kea during April and May 1998. We placed a rat snap trap at each station along transects 121, 116, 120, 119, and 118 (n = 78; Figure I.3). We alternated trap locations between stations, either on the ground or a horizontal limb of the closest live māmane tree. To avoid the possible capture of birds, we constructed hardware cloth exclosures (30 x 15 x 15 cm) with a low entrance that allowed passage for rats and mice but not a hopping bird. We baited the traps with Eaton peanut butter-flavored census bait blocks.

We also present the basket-trapping results from summer 1999 (see Chapter 35: Impacts of Predators on Bird Nests). Although this study was focused on the effects of rodent depredation on bird nests, the rodent capture rates provide additional relevant data on rodent abundance in subalpine Mauna Kea. There were two grids of 121 Haguruma® basket traps (242 total traps) set in māmane and māmane-naio woodland on the western slope of Mauna Kea for a total of 2,360 trap-nights.

Results

We captured mice and rats during each biannual survey; except in winter 2004 when we caught no rats. Rat capture rates remained low from summer 2000 through summer 2004, while *M. musculus* capture rates varied over fourteen-fold for the first nine surveys (Appendix, Figure 33.1). Both rat and mouse capture rates during the winter 2005 survey were the highest we recorded. The winter 2005 rat capture rate was six times greater than the rat capture rate for summer 2004, the survey with the next highest capture rate. The winter 2005 mouse capture rate was 1.7 times greater than any other capture rate recorded. We did not catch any other rodent species.

We caught mice in both mouse and rat traps in every survey session. Over the entire study, 86% of mice were caught in mouse traps and 14% were caught in rat traps. Over all ten surveys, we captured one rat in a mousetrap.

We trapped extensively for rodents in four habitat types (Jacobi 1989; Table 33.1). We trapped mice in all habitat types (*Sophora*, mixed forest, *Myoporum*, and pasture) and rats in the three forest habitats, but not the pasture. Over these five surveys, the mean capture rate of mice was significantly different across habitat types because of their low capture rate in pastures (two-factor ANOVA, $F_{3,12}$ = 8.26, P = 0.003; Figure 33.2). Capture rates of mice were lowest in the pasture in all seasons and years, except for summer 2002, when the capture rate in *Myoporum* habitat was slightly lower than the pasture (1.5 and 1.6 individuals/100 CTN, respectively). We found a significant difference in capture rates between pasture and non-pasture stations (Wilcoxon test, Z = 2.30, P = 0.02).

We could not evaluate habitat associations of rats in the same way as we did for mice because of very low capture rates in the transect study. However, our 2003 targeted study of rat effects on ʽiliahi strongly suggested a higher abundance of rats around this rare, native tree (Table 33.2). The ʽiliahi rat trap grid captured rats at over seven times the rate of the transect traps operating at the same time.

We caught mice throughout all elevations (1,811–3,021 m). However, we caught rats only below 2,600 m. We found no relationship between the numbers of mice caught per trap with

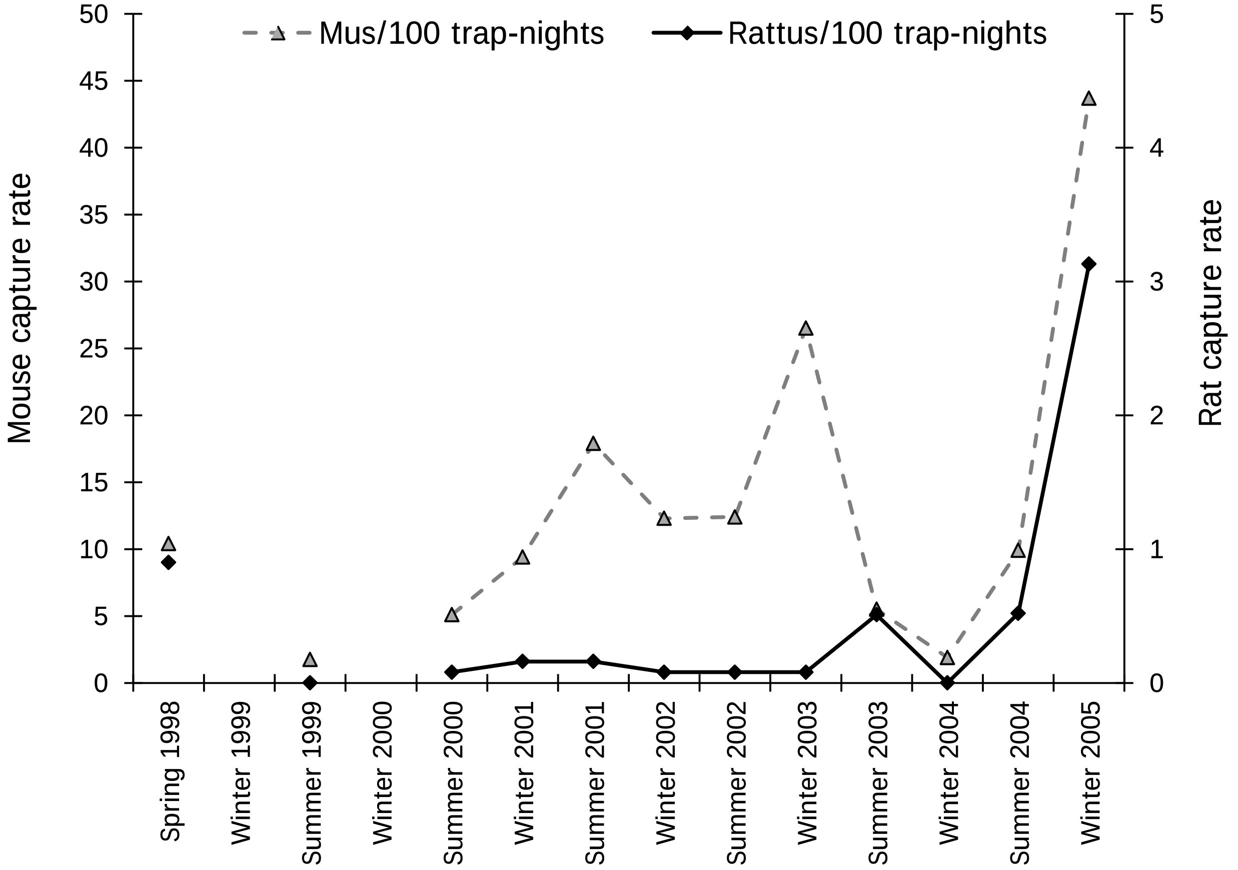

Figure 33.1. Capture rates (animals/100 corrected trap-nights) of mice (*Mus musculus*) and rats (*Rattus rattus*) on the western slope of Mauna Kea, Hawai'i, 2000–2005. For comparison, capture rates are also provided for spring 1998 (663 uncorrected trap-nights, arboreal and ground snap traps for both species) and summer 1999 (424 uncorrected trap-nights, ground basket traps for both species). No data were collected in winter 1999 or 2000.

Table 33.1. Corrected trap-nights for mice (*Mus musculus*) per habitat type over five surveys on the western slope of Mauna Kea, Hawai'i, 2000–2002.

	2000	2001		2002	
Habitat	Summer	Winter	Summer	Winter	Summer
Sophora	1,830.5	1,849.0	1,800.5	1,811.0	1,819.5
Mixed	1,373.0	1,371.0	1,347.0	1,344.0	1,334.5
Myoporum	305.0	282.5	273.5	280.5	273.0
Pasture	272.5	304.5	305.0	306.0	311.5

elevation in the first five survey seasons (linear regression, all $P > 0.81$). A two-factor ANOVA of mice/100 CTN did not indicate a significant effect of season on mouse abundance ($F_{1,7} = 0.24$,

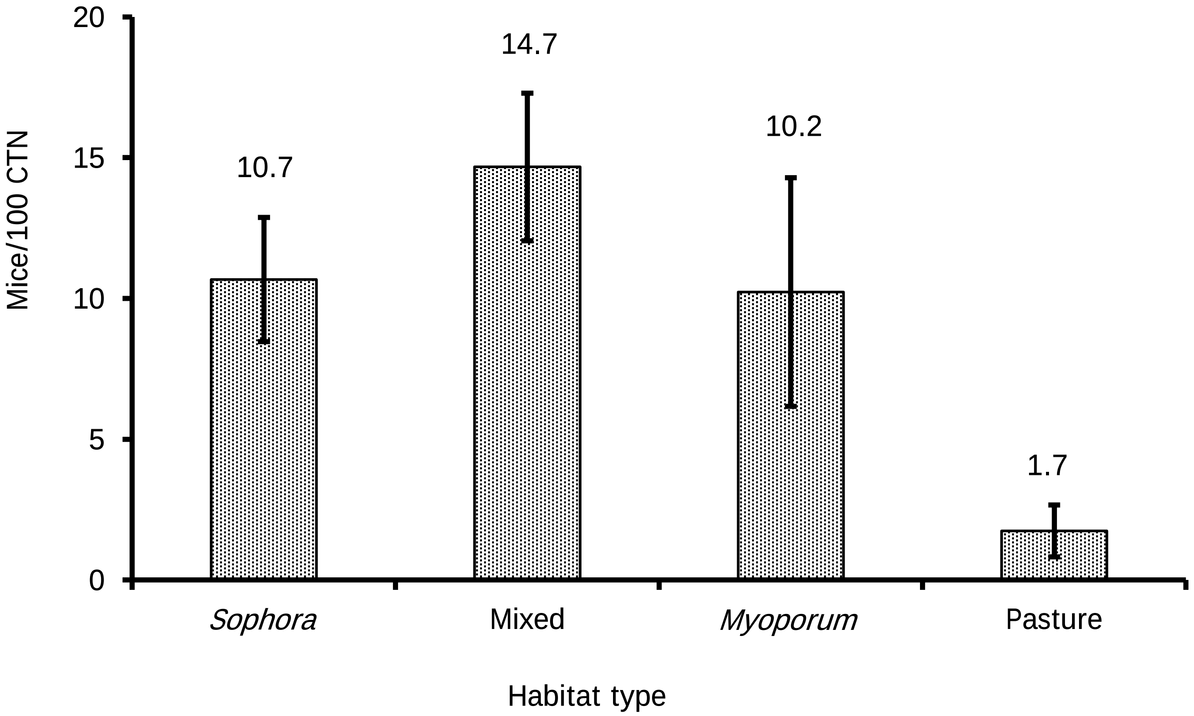

Figure 33.2. Mean capture rate (mice/100 CTN [corrected trap-nights] ± SE) of mice (*Mus musculus*) in four habitat types on the western slope of Mauna Kea, Hawai'i, 2000–2002.

Table 33.2. Capture rates of mice (*Mus musculus*) and rats (*Rattus rattus*) associated with a *Santalum paniculatum* grove and a control grid in mixed *Sophora-Myoporum* forest. The data from the rodent transects on the western slope operating at the same time are presented for comparison. CTN = corrected trap-nights.

	Santalum	*Sophora-Myoporum*	Rodent transects
Corrected trap-nights	353.0	349.5	1,213.0
Mus musculus (*n*)	4	9	971
Mus / 100 CTN	1.1	2.6	26.5
Rattus rattus (*n*)	2	0	1
Rattus / 100 CTN	0.60	0.00	0.08

P = 0.64). We did not find a significant relationship (two-sample t-test, t = -1.83, *P* = 0.32) between rodent abundance and median rainfall six months prior to each survey.

The proportion of mouse age/sex classes was relatively constant over the first five rodent surveys (Figure 33.3). Adult males were the most abundant, and adult females were the second most abundant. The adult males weighed 13.0 ± 0.1 g, and females weighed 13.8 ± 0.2 g. Juvenile females and males were found in similar abundance, but were always less abundant than adults. Juvenile males weighed 9.6 ± 0.1 g, and juvenile females weighed 8.8 ± 0.1 g.

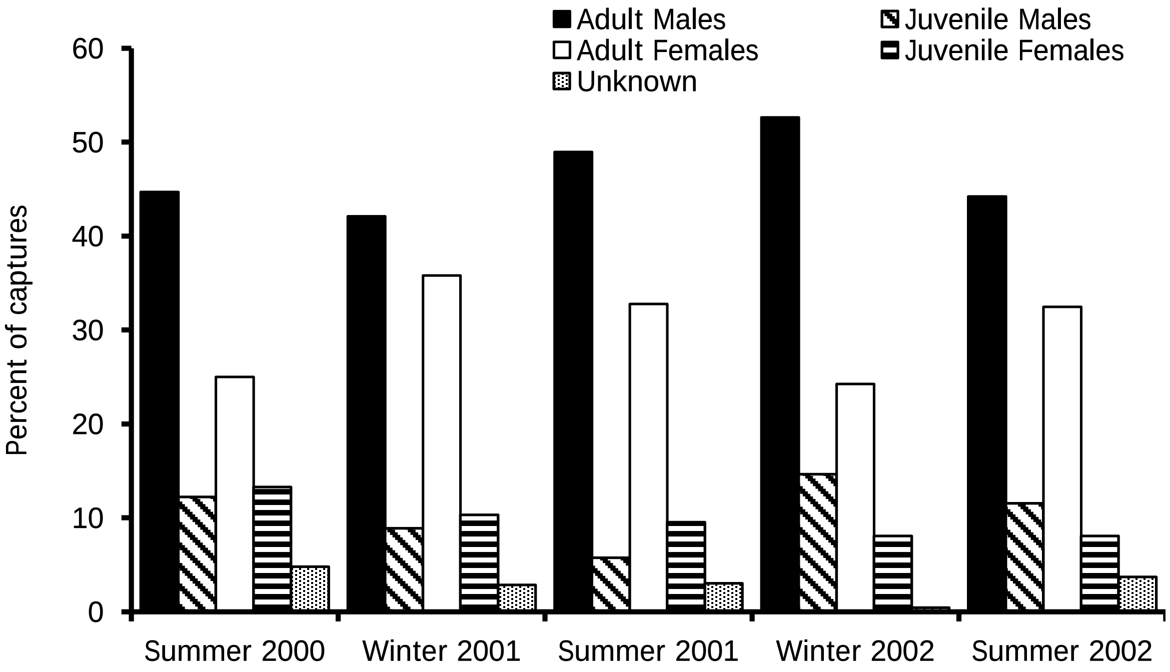

Figure 33.3. Mean proportion of each age/sex class of mice (*Mus musculus*) caught over five surveys on the western slope of Mauna Kea, Hawai'i, 2000–2002.

Using a general linear model, we found that the factors affecting the dependent variable (ln[mouse weight]) were age, age:season interaction, and age:sex interaction (Table 33.3).

Table 33.3. Factors affecting mouse (*Mus musculus*) weight on the western slope of Mauna Kea, Hawai'i, 2002–2003.

Factor	Coefficient	*t* -value	*P*
Intercept	2.399	404.65	–
Winter	-0.010	-1.68	0.338
Juvenile	-0.174	-29.30	0.000
Female	0.002	0.30	0.808
Juvenile in winter	0.012	2.06	0.029
Juvenile female	0.050	0.63	0.000

We caught rats from every age/sex class. The average weight for adult females was 101 ± 8.1 g (± SE; *n* = 6), and adult males was 172 ± 36.0 g (*n* = 7). Juvenile females weighed 60 and 92 g (*n* = 2), and juvenile males weighed 60 and 122 g (*n* = 2).

We captured pregnant mice in the five surveys when we checked for female reproduction, but we did not catch pregnant rats in those surveys. Pregnancy rates and number of embryos in mice varied greatly (Table 33.4). The winter and summer 2004 surveys indicated a significant difference ($P < 0.001$) between the anal-genital distances in males: 12 ± 1.2 mm (± SE; $n = 91$) and females: 7 ± 0.2 mm ($n = 86$).

Table 33.4. Mouse (*Mus musculus*) pregnancy rates and average number of fetuses on the western slope of Mauna Kea, Hawai'i, 2002–2004.

Season	Pregnant mice (%)	Average number of fetuses (± SE)
Summer 2002	73/150 (48.7)	5.9 ± 0.21
Winter 2003	1/85 (1.2)	8.0
Summer 2003	17/28 (60.7)	4.2 ± 0.29
Winter 2004	1/4 (25.0)	6.0
Summer 2004	21/48 (43.7)	2.9 ± 0.79

The comparison of mouse detection by census block versus trapping data for the summer 2000 survey indicated a difference in the mean probability of mouse presence (trap = 0.25 ± 0.11; census block = 0.11 ± 0.32). Mice visited both snap traps and census blocks at 404 (73.3%) of the stations. Because we seldom caught rats, and the evidence of rat gnawing on census blocks was hard to detect in the presence of mice gnawing, we could not compare trapping and census block methods of surveying the rat population.

During the arboreal activity study we trapped during 7 April–15 May 1998 on the northern slope, yielding 663 uncorrected trap-nights. We caught 69 total mice (10.41 mice/100 trap-nights), 45 in ground traps (65%) and 24 in tree traps (35%). We caught six rats (0.90 rats/100 trap-nights), four in ground traps (67%) and two in tree traps (33%).

Discussion

The changes in mouse abundance over all ten surveys did not seem directly dependent on season (winter or summer), but there might have been a subtle non-seasonal population cycle (Tomich 1986). Mouse and rat capture rates were high throughout the winter 2005 survey (Appendix), indicating an intense population irruption during that time. The magnitude and length of the irruption were greater than any other recorded since the 1970s (P. Tomich, Hawai'i Department of Health [retired], personal communication).

Five surveys indicated that mice inhabited the *Sophora*, mixed, and *Myoporum* forests at similar abundances, but rarely utilized the pasture. Across all years we caught very few mice in the pasture where the grass cover was continuous. The scarcity of mice in the pasture may have been due to increased exposure to predators or to the scarcity of grass seed resulting from Kikuyu grass (*Cenchrus clandestinus*), a species that spreads vegetatively, dominating the pasture. Cattle grazing may also have kept grass seed availability low. Mouse abundance did not vary significantly in relation to elevation on the western slope. There was a positive, albeit non-significant, relationship between mouse abundance and six-month median precipitation.

Mouse weights differed significantly with age, an age:season interaction, and an age:sex interaction. The age:season effect may be explained by the fact that many young adults are not fully grown in their first winter. The possibility of adult females carrying fetuses, thus weighing more, may explain the age:sex interaction. We observed that adult female mice weighed more than adult males, which is inconsistent with other studies in Hawai'i (Tomich 1981). The significant difference in anal-genital distances between male and female mice will aid in sex determination during future studies, although some overlap in distances between the sexes indicates that anal-genital distance is not a definitive sexing tool.

We captured pregnant female mice in the five surveys when we examined female reproduction, indicating at least biannual breeding. Nevertheless, the pregnancy rate was higher in summer (49.1%) than in winter (2.2%). The pregnancy rate was higher in winter 2004 compared to winter 2003, but this might have been an artifact of the low sample size in winter 2004. Surveys for pregnant females during spring and fall would have indicated whether mice breed year-round on the western slope of Mauna Kea.

We found snap trapping to be a more sensitive method of detecting mouse presence than were census blocks, based on the mean probability of mouse detection. Even so, there were fewer than 50 instances (7.3% of station-nights) in which census blocks were more sensitive than snap traps in detecting mice. Our comparison of mouse detection methods did not independently compare census blocks with snap traps. To have done so would have required 1) monitoring a transect with one census block per station for four consecutive nights, then 2) monitoring the same transect with one snap trap per station over the following four consecutive nights. This method would yield temporally independent data and provide a more robust comparison of survey methods.

The scarcity of rats on the western slope was consistent with results of previous studies (Table 33.5) and may be attributable to depredation by carnivores and factors associated with high elevation, such as low temperatures or lack of water (Amarasekare 1994; see Chapter 32: Feral Cat and Mongoose Diet). Although we were unable to determine the relationship of rats to habitat type due to low capture rates, the frequency with which they were trapped near *Santalum* trees suggests some level of attraction. Our finding that both mice and rats exhibit arboreal activity agrees with results from Amarasekare (1993). Mice are not thought to be nest predators or competitors of palila (Amarasekare 1993), but we do not entirely discount their potential to cause disturbance to nesting birds. Video images of a mouse at the nest of a palila were recorded by a surveillance camera (see Chapter 9: Breeding Phenology, Productivity, and Nesting Success), although there was no indication of negative consequences.

Table 33.5. Capture rates of rats (*Rattus rattus*) in surveys on the western and northern slopes of Mauna Kea, Hawai'i.

Survey	Location	Date	Trap-nights	*Rattus* /100 trap-nights
van Riper (1978)	West	1973–75	2,442	0.38
Amarasekare (1994)	West	1990	3,328	0.66
U.S. Geological Survey *unpublished data*	West	1992	1,076	0.45
U.S. Geological Survey *unpublished data*	North	1992	515	0.78
U.S. Geological Survey *unpublished data*	West	1996	718	0.97
U.S. Geological Survey *unpublished data*	North	1996	1,162	0.26

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Appendix. Date, Effort, and Capture Rates of Mice (*Mus musculus*) and Rats (*Rattus rattus*) on the Western Slope of Mauna Kea, Hawai'i, 2000–2005.

	Mus musculus					*Rattus rattus*				
Session	Trap-nights	Sprung traps	Corrected trap-nights†	Number captured	*Mus*/100 trap-nights†	Trap-nights	Sprung traps	Corrected trap-nights†	Number captured	*Rattus*/100 trap-nights†
Sum 2000	3,840	168	3,756.0	186	5.0	1,280	50	1,255.0	1	0.08
Win 2001	3,840	115	3,782.5	354	9.4	1,280	37	1,261.5	2	0.16
Sum 2001	3,840	235	3,722.5	670	18.0	1,280	61	1,249.5	2	0.16
Win 2002	3,840	198	3,741.0	461	12.3	1,280	54	1,253.0	1	0.08
Sum 2002	3,840	203	3,738.5	462	12.4	1,280	20	1,270.0	1	0.08
Win 2003	3,840	365	3,663.5	968	26.4	1,280	134	1,213.0	1	0.08
Sum 2003	1,800	128	1,736.0	95	5.5	600	34	583.0	3	0.51
Win 2004	1,794	106	1,741.0	33	1.9	598	31	582.5	0	0.00
Sum 2004	1,800	133	1,733.5	172	9.9	600	41	579.5	3	0.52
Win 2005	1,796	400	1,596.0	698	43.7	599	111	543.5	17	3.13
Total	30,230	2,051	29,210.5	4,108	14.1	10,077	573	9,790.5	31	0.32

†Capture effort and rates corrected according to Beauvais and Buskirk (1999)

34 FORENSIC TECHNIQUES FOR PREDATOR IDENTIFICATION

Daniel M. Goltz, Paul C. Banko

Introduction

Introduced mammals, particularly feral cats (*Felis catus*) and black rats (*Rattus rattus*), may limit palila (*Loxioides bailleui*) populations by preying on eggs, chicks, and adults (van Riper 1980; Pletschet and Kelly 1990; Lindsey *et al*. 1995; Banko *et al.* 2002, 2009; Hess *et al.* 2004). Feral cats are relatively abundant in Palila Critical Habitat (Goltz *et al.* 2008) and may impede the recovery of palila (U.S. Fish and Wildlife Service 2006). Although rat abundance is relatively low in the subalpine environment of Mauna Kea, their effect on the palila population should not be underestimated or dismissed (Amarasekare 1993; see Chapter 33: Rodent Survey). Predation is, by its nature, difficult to document because the prey may be entirely consumed or the cause of death may be obscured, making scavenging difficult to distinguish from predation. In addition, many predators are elusive and difficult to observe.

We conducted studies to determine the frequency of predation and its consequences for palila demography. We tracked predator movements to establish their home range characteristics and activity patterns (Goltz *et al*. 2008; see Chapter 31: Feral Cat Home Range and Movements). We also determined the diet composition and foraging behavior of small mammals to help understand their role as predators (Hess *et al.* 2004, 2007; see Chapter 32: Feral Cat and Mongoose Diet). Monitoring the impact of predators at palila nests using surveillance cameras can also provide critical insights (Laut *et al.* 2003; see Chapter 11: Behavior at Nests). The combination of these different approaches can help determine the importance of predators in limiting the survival and reproduction of palila; but, to develop effective predator management strategies, it is necessary to know what predators to target.

Previously, we recovered 11 depredated palila from the northern slope of Mauna Kea during translocation 2 in 1997–1998 (see Chapter 2: Translocating Wild Palila). Often the remains were reduced to a pile of feathers or had been scavenged post mortem, making an identification of the predator difficult. To help identify mammalian predators of palila whose carcasses were found in the wild, we initiated this study to help recognize diagnostic clues left by different species. Our approach was to observe predators feeding on the carcass of a small bird in a controlled setting to determine whether the predator could be identified solely by clues observed on the carcass. We observed predator feeding habits, videotaped their behavior, and described and cataloged the remains. We used this information to develop methods and skills for identifying species responsible for nest destruction and bird mortality.

Methods

We built a wooden feeding cage (60 x 60 x 60 cm) with a one-way glass window on one side and a sliding door on the opposite wall. The sliding door allowed the predator to be transferred to the feeding cage with minimal disturbance. A fluorescent light was mounted above the hardware cloth ceiling of the cage to facilitate observation of the predator and reduce its ability to see out the window. This design allowed us to observe the predator’s feeding behavior without the predator being aware of us.

Freshly killed red-billed leiothrix (*Leiothrix lutea*), a widespread introduced species, were fed to feral cats (*n* = 6 feedings to 3 feral cats), mongooses (*Herpestes auropunctatus*; *n* = 6 feedings to 3 mongooses), and black rats (*n* = 6 feedings to 2 rats). Feeding sessions were observed and videotaped when possible, and the red-billed leiothrix remains were collected and examined. Feral cats and mongooses were fasted for a period of 12–36 hours preceding a feeding session. Rats were fasted for a 12-hour period before the feeding sessions. In most cases, predators began feeding soon after being placed in the feeding cage.

Results

Rat Feeding Behavior

Rats (*n* = 2) began eating their bird either by entering the head through an eye socket (*n* = 4 occurrences) or by entering the stomach cavity (*n* = 2 occurrences). In cases where the head was eaten first, one eyeball was removed and the inner contents consumed. The iris and outer tissue were always discarded. Next, they chewed open the area around the eye socket and ate the brain. The other eye was then pulled through the same opening and eaten in the same manner as the first eye. Occasionally, rats also ate some of the neck muscles and gnawed on the beak. When beginning with the body of the bird, the rat bit the breast several times before parting the feathers and chewing into the stomach cavity. Rats usually removed and discarded the stomach, intestines, gizzard, and crop. Other internal organs were eaten next, followed by the pectoral and leg muscles.

Rats consumed the bird in about one hour after feeding began. The crop, outer eyeball tissue, gizzard, intestines, and a large pile of body feathers generally constituted the remains of the bird after being eaten by a rat. The skull was usually left attached to the body, with the brain and eyeballs always eaten. Sometimes skin and feathers remained attached to the outside of the skull. Both wings were always intact and either attached or detached from the body. Legs and feet were usually attached to the pelvic girdle. Entrance to the stomach cavity from the sternum was always apparent.

Mongoose Feeding Behavior

Mongooses (*n* = 3) first bit the head of the red-billed leiothrix several times, crushing the skull, beak, and brains. With the head still attached to the body, mongooses then chewed off and ate the entire head and neck. They then usually stood on the bird's body with one or two front feet, tearing out and eating the remainder of the neck and the vital organs through the opening in the furculum. This was followed by tearing off and eating the pectoral muscles, sternum, keel, and wings. Mongooses usually chewed off the wings where they attached to the body and ingested the bones, meat, skin, and feathers up to the wrist. The outer 4–6 primaries were chewed off as one unit at the wrist and fell in a pile. Occasionally the entire wing, including the flight feathers, was eaten. Internal organs, pelvic girdle, and legs were eaten in the same manner as the breast and sternum. Tail feathers were usually eaten completely. The remains of the bird mainly consisted of flight feathers, which sometimes appeared plucked (pulled out of dermis; shaft complete), or cut (shaft severed evenly and neatly). Commonly four to six outer flight feathers were clumped together. Several body feathers, usually from the breast, were also included in the remains.

Feral Cat Feeding Behavior

Feral cats (*n* = 3) usually sniffed the freshly killed red-billed leiothrix carcass several times before picking it up in their mouths and consuming it. They ate the entire bird, except for the flight feathers and occasionally the feet, very rapidly. Compared to remains left by mongooses and rats, those left by feral cats were minimal and appeared highly processed. The flight feathers were usually separated and the shafts appeared cut. On one occasion, both wings were found entire in the remains. Usually one or both feet were recovered in the remains, sometimes attached completely or partially to the legs. Body feathers were absent or rare in the remains.

Discussion

Results of this study were invaluable in identifying predators of palila during translocation trials and nesting seasons. Complementary studies of the feeding behavior of avian predators, pueo (*Asio flammeus sandwichensis*) and ʽio (*Buteo solitarius*), would be helpful in understanding the impact of the entire suite of predators on Mauna Kea.

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35 IMPACT OF PREDATORS AT BIRD NESTS

Daniel M. Goltz, Paul C. Banko

Introduction

Introduced, small mammals threaten native Hawaiian birds, especially at nests, but predator impacts on birds are often difficult to document due to their secretive behavior, generally small populations, and the logistical challenges of monitoring nests in trees. Nevertheless, in the subalpine woodlands of Mauna Kea, bird nests are relatively easy to monitor due to the generally small size of trees and the abundance of birds that sometimes breed for many months. Feral cats (*Felis catus*) and rats (*Rattus rattus*) have been identified as the major predatory threats to the endangered palila (*Loxioides bailleui*), particularly at nests (Pletschet and Kelly 1990; Banko *et al.* 2002, 2009; Hess *et al.* 2004, 2007), but their effects are not easily quantified. Moreover, the impacts of other potential predators are obscure. As part of our effort to evaluate predator impacts on the endangered palila, we initiated this pilot study to develop methods for identifying nest predators and for relating rat and mouse (*Mus musculus*) abundances to the incidence of nesting failure in different forest types.

Methods

In February 1999, we established two grids on the western slope of Mauna Kea for intensive surveys of rodents and to monitor the fate of active bird nests. Each grid measured 500 x 500 m (25 ha). We situated the grids to avoid overlap with existing nest searching transects (see Chapter 9: Breeding Phenology, Productivity, and Nesting Success) and to sample two distinct forest types, māmane (*Sophora chrysophylla*)-dominant and mixed naio (*Myoporum sandwicense*)-māmane. The grids consisted of 11 parallel transects with stations every 50 m. Stations were located with the use of a GPS and were marked with flagging. A Haguruma® wire basket trap was placed at each station for a total of 121 basket traps per grid. Traps were placed either on a low limb or on the ground near woody vegetation, based on results of past trapping efforts. The traps were pre-baited with shredded coconut for three days before we baited with fresh coconut chunks. We checked the traps daily.

To determine avian productivity rates, a crew of two to four people systematically searched both grids with equal effort during March and April of 1999. All nests were marked and a distinction was made between old nests from previous breeding seasons and active nests (nests under construction or those containing eggs or chicks). Active nests were monitored with the aid of a pole-mounted mirror at least once each week to determine their fate. Tracking boards (30 x 60 x 0.6 cm plywood) were placed on the ground, surrounding the trunks of three active nest trees. Two varieties of tracking boards were tested: 1) a light coat of fine sand on lubricating grease and 2) hair spray applied over masonry coloring agent. When a nest failed, we systematically examined the nest, its contents, the nest tree, and the surrounding area for evidence of the cause (predator or other). All palila nests, including those outside the grids, were checked daily from the time of location through fledging or failure. If a nest that previously contained eggs or chicks was found to be empty before the predicted fledge date, it was assumed to have failed and was examined for possible causes.

One palila nest that failed during the 1999 breeding season was under surveillance with a video camera, and the predator was easily identified. Other nest failures were investigated carefully by examining the nest, the nest tree, and the ground below the nest (within a 20-m radius of the nest tree) for signs of disturbance, blood, and remains of the nest contents, as well as mammalian tracks, hair, and feces.

Results

Basket traps on the māmane-dominant grid were set for 424 trap-nights during 16–25 June 1999. During that period, four mice (0.94 mice/100 trap-nights) and no rats were captured. Traps on the mixed naio-māmane grid were set for 1,936 trap-nights during 6 April–25 June 1999, and 34 mice (1.76 mice/100 trap-nights) and no rats were captured.

Nest Predation in 1999

We searched for bird nests in the mixed naio-māmane forest grid for two weeks beginning 23 February 1999. We located and monitored 14 active nests (13 Hawai'i 'amakihi [*Hemignathus virens*] and one Hawai'i 'elepaio [*Chasiempis sandwichensis*]) of which three (21.4%) fledged at least one chick, eight (57.1%) failed due to predation, and three (21.4%) failed for unknown causes (Figure 35.1).

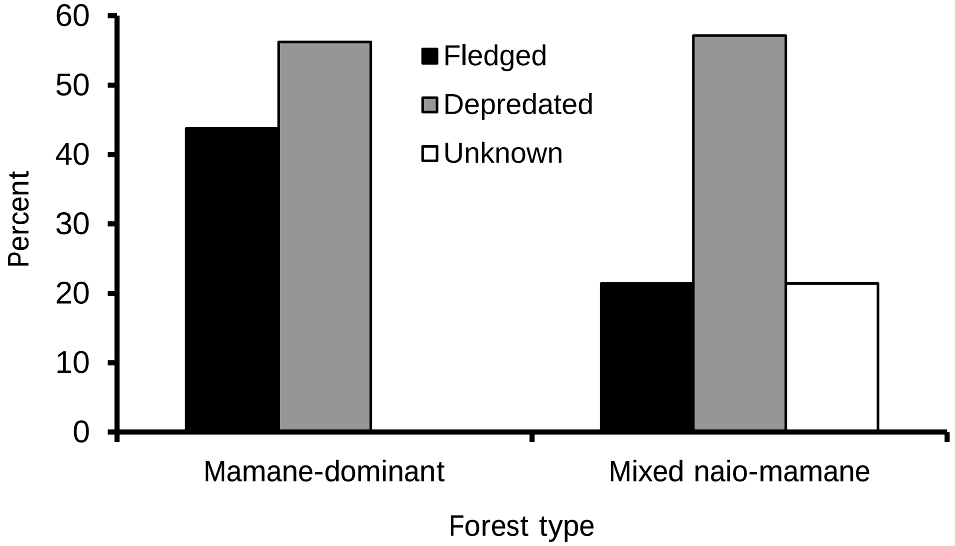

Figure 35.1. Avian nest productivity in māmane-dominant and mixed naio-māmane forests on Mauna Kea, Hawai'i, 1999–2000.

We searched for nests in the māmane-dominant grid for two weeks beginning 10 March 1999. We located and monitored 16 active nests (15 Hawai'i 'amakihi and one house finch [*Carpodacus mexicanus*]) of which seven (43.8%) fledged at least one chick and nine (56.3%) failed due to predators.

The tracking boards yielded no useful information. Both methods (sand on grease and hair spray on masonry coloring agent) were placed at the bases of three separate trees with active nests. An unknown predator depredated one nest, but no tracks were visible on the boards.

During the 1999 breeding season, predators destroyed 6 of 37 (16.2%) active palila nests found outside our two study grids. The evidence we observed indicated that four of the nests were depredated by feral cats (*Felis catus*), one nest may have been depredated by a pueo (*Asio flammeus sandwichensis*), and one nest was probably depredated by a rat. Details of these nest failures are provided in the following accounts:

- *Nest 99.011* was being monitored by video camera on 22 June when a cat climbed to the nest and killed both 13-day-old nestlings. The cat did not consume either nestling. One was picked up in the cat's mouth, crushed, and dropped to the ground. The other nestling was swatted with a paw and left in the nest. There was no noticeable damage to the nest.
- *Nest 99.034* was depredated on 21 July when two eggs were being incubated. One egg was found broken on a limb just beneath the nest, and the embryo of the other egg was found on the ground beneath the nest with eggshell fragments attached to it. No tracks, hair, or feces were found in or near the tree, leading us to suspect that a rat was the predator.
- *Nest 99.044* was depredated on 4 August, a day after the two chicks hatched. No remains of the chicks were located. The nest was not disturbed, and we found no tracks, hair, or feces near the nest, which was very exposed and visible. A pueo was seen hunting in the area on 3 August, and it may have been the predator.
- *Nest 99.052* was depredated by a cat on 8 August. Remains of the single 10-day-old chick were found, and they closely resemble those associated with nest 99.011. Cat hair was found in the tree and cat tracks were present near the tree.
- *Nest 99.055* contained one 13-day-old chick when it was depredated on 28 August. The video camera at this nest failed to record the event due to a power failure. Remains of the chick were located near the base of the tree and were consistent with other cat kills. The chick was partially eaten, and the remains included the head, crop, and intestines.
- *Nest 99.065* was depredated on 27 August, a day after we banded both 14-day-old chicks. The nest cup had been removed and was found on the ground. Cat hair was found on a limb beneath the nest. Remains of both chicks were consistent with those of other cat kills.

Nest Predation in 2000

Four of 36 (11%) active palila nests failed due to predation during the 2000 breeding season. Remains at three of the nests strongly implicated feral cats as the predators. The fourth nest may have been depredated by a pueo. Details of these nest failures are provided in the following accounts:

- *Nest 00.003* was depredated on 23 June, when it contained two 11-day-old nestlings. One nestling, missing its head, was found at the base of the tree, which could not be climbed for further investigation. The remains were consistent with other cat-depredated nests.
- *Nest 00.008* contained two 15-day-old nestlings when it was depredated on 16 June. Both nestlings were discovered in a mangled state beneath the nest and cat hair was found on tree limbs near the nest.
- *Nest 00.030* contained two 16-day-old nestlings when it was depredated on 31 July. This nest was situated 0.5 m above ground in a clump of grass at the base of a māmane tree. Cat hair was found near the remains of the nestlings and cat tracks were observed leading up to the nest.

- *Nest 00.046* probably contained two 1-day-old nestlings when it was depredated on 31 July. The nest was empty and the nest lining was slightly disturbed. No hair or tracks were seen in the nest tree or surrounding area, suggesting that a pueo may have been the predator.

Discussion

Our failure to capture rats in 2,360 trap-nights on the two study grids supports earlier findings of low rat density on the western slope. The lack of trapping success could reflect seasonal or annual variation in rat population levels or a decline in rat densities due to drought conditions that prevailed during the study.

Mouse abundance was also lower in our study than has been reported previously (Amarasekare 1994; see Chapter 33: Rodent Survey). Low abundance supports the idea that drought may have depressed rodent populations during the 1999 breeding season. Mice are not known to be predators or competitors of palila (Amarasekare 1994), but mice climb trees and may disturb palila at their nests, especially during the egg stage. In addition, owls prey on native birds on Mauna Kea (Snetsinger *et al.* 1994, Klavitter 2009). Detecting the impact of these predators, however, is much more problematic than for mammals because they may leave no trace at nests. In such cases, it may be difficult or impossible to confirm depredation of specific nests by owls without the use of surveillance cameras.

Predation at nests on both study grids occurred at similarly high levels (56.2% in the māmane-dominant and 57.1% in the naio-dominant forest). However, fledgling production was nominally higher on the māmane-dominant grid, where 43.8% of nests fledged at least one chick, than on the naio-dominant forest grid, where 21.4% of nests fledged a chick. Three nests in the naio-dominant grid possibly were abandoned due to prolonged rain and cold weather in late February 1999.

A checklist and protocols for evaluating depredated palila nests was not available during 1996–1998. Nevertheless, reviewing our field notes in light of information gained during this study suggests that 2 of 50 (4%) active nests in 1996 were depredated by cats, and one was depredated by a pueo. In 1997, 1 of 12 active nests was likely depredated by a pueo, and one was destroyed by an unknown predator. In 1998, 1 of 21 (4.8%) active nests was depredated by a cat, and unknown predators destroyed four others. One (Nest 01.006) of 10 active palila nests monitored during the 2001 breeding season was depredated by a feral cat, which was recorded on video, climbing to the nest and killing the single 13-day-old chick. The adult palila returned to the nest within 20 minutes and removed the dead chick. In 2002, pueo were likely involved in the failure of two palila nests. Pueo were observed twice near Nest 02.010 in the eight days prior to nest failure. The nest was in a pilo (*Coprosma montana*) tree near a grassy open area and contained two 4-day-old chicks when it failed. One chick was found dead, clutching lichen, about 10 cm from the nest rim with no apparent physical injuries. The other chick was never found. There were no signs of mammalian predators in the area. At Nest 02.016, two chicks disappeared at less than one week of age; yet no signs of predation were detected. Thus, although the data do not support a detailed analysis, feral cats and pueo may have depredated palila nests at roughly similar levels.

The two types of tracking boards we placed at nests were not suitable for detecting predators. We suspect that rodents could have crawled underneath boards or that animals were too light to imprint the tracking substrate. Cats could have jumped over the narrow boards to reach the tree trunk. We developed a checklist and protocols to evaluate evidence of predation at failed nests to standardize predator identification. Even so, the use of surveillance cameras probably would yield more reliable results.

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36 PREDATOR MANAGEMENT

Daniel M. Goltz, Raymond M. Danner, Steven C. Hess, Chris Farmer, Kevin W. Brinck, Paul C. Banko

Introduction

Depredation by introduced mammals is often postulated as an important cause of the decline in Hawaiian birds and as a major factor limiting populations of endangered forest birds (Atkinson 1977, Berger 1981, van Riper and Scott 2001, Banko and Banko 2009, Lindsey *et al*. 2009). On Mauna Kea, carnivores, including the feral cat (*Felis catus*) and small Indian mongoose (*Herpestes auropunctatus*) and rodents, including the black rat (*Rattus rattus*) and house mouse (*Mus musculus*), occupy the critical habitat of the endangered forest bird, palila (*Loxioides bailleui*). Palila may be especially susceptible to depredation by introduced mammals since their reproductive strategy evolved in the absence of mammalian predators and their nests have a strong odor (van Riper 1980, Pratt *et al*. 1997) that may attract mammalian predators that rely on olfactory cues (Westmoreland and Best 1985).

This study and others (van Riper 1978; Pletschet and Kelly 1990; Amarasekare 1994; Snetsinger *et al.* 1994; Pratt *et al*. 1997; Banko *et al.* 2002; Laut *et al.* 2003; Hess *et al.* 2004, 2007a; see Chapter 35: Impact of Predators at Bird Nests) document various types of evidence of predation by feral cats and rats on native birds, including the palila and their nestlings and eggs on Mauna Kea. Mongooses are also implicated in the deaths of palila and other passerines based on observation of remains and analysis of digestive tracts (see Chapter 32: Feral Cat and Mongoose Diet). Research into the ecology of the palila and small mammal species on Mauna Kea indicates that palila populations would benefit significantly from a sustained predator control program. The goal of this study is to help develop strategies and refine techniques for reducing threats from introduced predators.

Methods

We tested techniques for removing predators on the northern and western slopes of Mauna Kea during 1998–2005. Methods for reducing feral cat and mongoose numbers focused on the effectiveness of different spatial and temporal distributions of live traps. Research into reducing rat threats consisted of varying the placement and duration of poison baits. The ultimate response variable of interest for both rats and carnivores was the effect of different treatments on the depredation of palila. Nevertheless, due to personnel limitations, we used predator abundance as a proxy for depredation rate.

Predators were removed in nine experimental sessions. Sessions 1, 3, 8, and 9 were conducted on the northern slope, while sessions 2 and 6 were on the western slope. These sessions focused on determining predator abundance and immigration rates using various trap arrays. We trapped carnivores during session 7 to determine how mammal abundance differed one year after an intense trapping effort (session 6) ended in the same area. During sessions 4 and 5, we trapped and released cats for a radio-tracking study (Goltz *et al.* 2008; see Chapter 31: Feral Cat Home Range and Movements). Additionally, to test rat removal methods, we applied poison baits in three trials within a 1-km^2 area on the northern slope (predator grid) before and during translocations 3, 4, and 5 (fall 1998, winter 2004, and winter 2005 respectively; see Chapter 2: Translocating Wild Palila).

During the carnivore removal trials, we used Tomahawk® model 106 live traps (66 x 23 x 23 cm). We covered all traps with plastic sheets and placed a cloth inside to serve as bedding.

We baited the traps with canned cat food. Occasionally we substituted raw eggs, canned sardines, or mackerel in an attempt to entice wary cats or mongooses that may not have been attracted to canned cat food. When traps were not in use, we wired the doors open. When traps were in use, we checked them daily.

We designed our trapping arrays based on cat movement data (Goltz *et al.* 2008; see Chapter 31: Feral Cat Home Range and Movements). Long sessions on the northern slope (sessions 3, 8, and 9; Table 36.1) effectively trapped an area of approximately 1,800 ha, which included a boundary strip half the diameter of a cat's circular home range around the trapping area (Whitford 1976). Long sessions on the western slope (sessions 6 and 7) covered approximately 2,500 ha. The effective trapping area for mongooses was smaller than the entire area within the trapping array, based on data from Tomich (1969) that suggested the average home range diameter for mongooses was smaller than the typical distance between our traps. Depending on the objectives of each trapping session, we varied the distance between traps, location of traps in relation to the trees that marked the stations, and operation (i.e., whether a specific trap was open or not). Trap spacing was similar for sessions 3, 8, and 9, and trap spacing was similar for sessions 6 and 7.

Table 36.1. Date, location, and trapping effort for feral cats (*Felis catus*) on the western and northern slopes of Mauna Kea, Hawai'i, 1998–2005.

Session	Date	Slope	Traps (*n*)	Trap-nights
1	30 Apr–2 Jul 1998	North	26	229
2	28 Jul–20 Aug 1998	West	25	355
3	10 Sep 1998–4 Mar 1999	North	65	2,628
4	15 Jun–15 Jul 1999	West	47	170
5	18–29 Sep 2000	West	48	281
6	9 Apr–31 Aug 2002	West	105	3,130
7	30 Jun–13 Aug 2003	West	105	651
8	4 Nov 2003–16 May 2004	North	62	2,128
9	13 Nov 2004–7 July 2005	North	62	2,208
Total				11,736

During session 1 we set carnivore traps on Hawai'i Forest Bird Survey (HFBS) transects 121, 116, 119, and 118 on the northern slope (Table 36.1, Figure 36.1). On each transect, we placed a trap at the highest elevation station, the center elevation station, and the lowest elevation station.

Traps set during session 1 ranged from 2,149–2,935 m elevations. We set an additional eight traps in locations where we opportunistically found cat tracks and another eight in the area of high palila roosting activity (east of HFBS transect 116, at approximately 2,350 m elevation). During session 2, we placed 25 traps along dirt roads in core palila habitat on the western slope. Traps were spaced about 1,600 m apart and within 10 m of the road. During session 3, we placed 25 traps in the predator grid on the northern slope. In order to intercept immigrants, we also placed 19 traps along a perimeter loop that included HFBS transect 121, a trail at tree

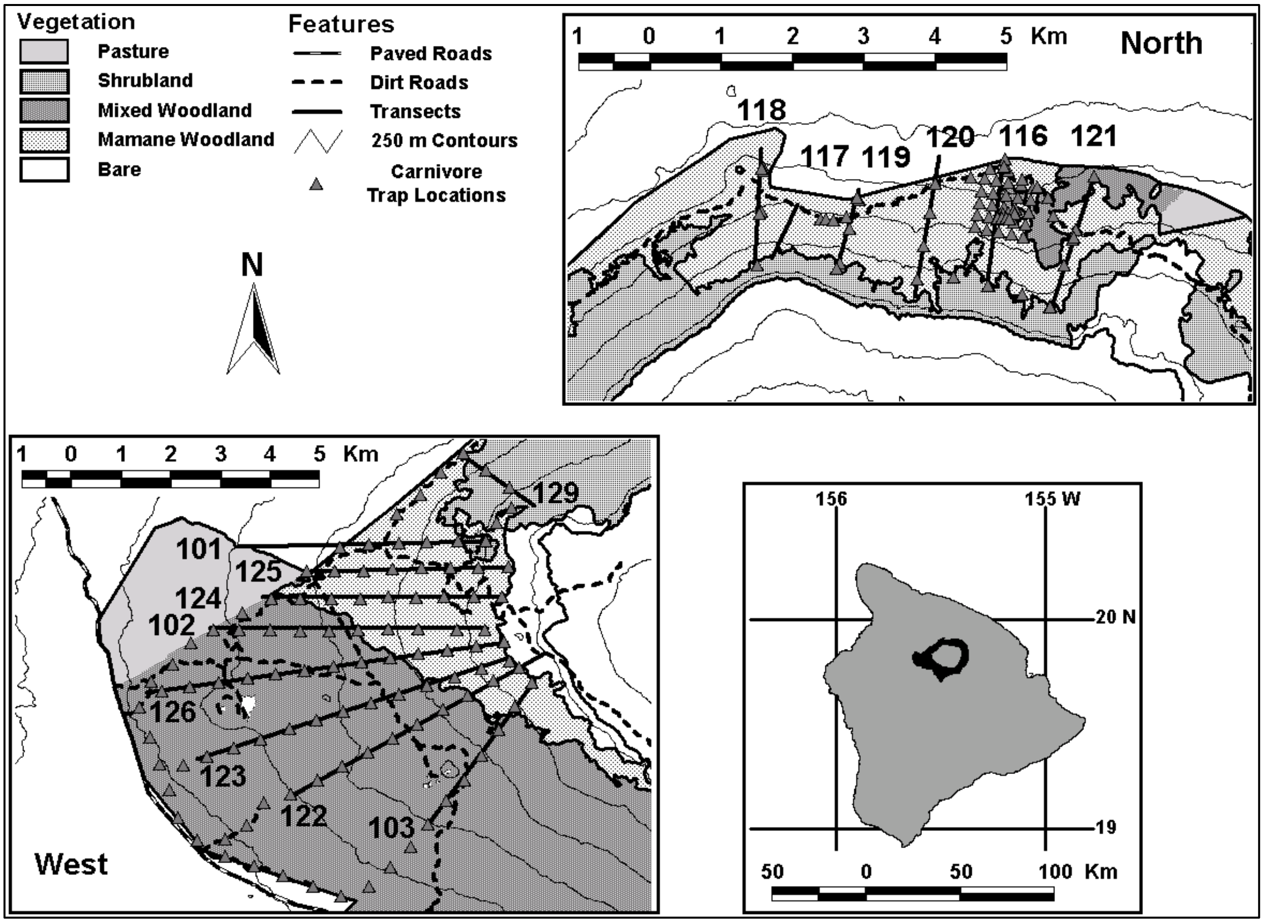

Figure 36.1. Carnivore trap locations on Mauna Kea, Hawai'i, 1998–2005. Not all trap arrays were operational in any particular session (see text for details).

line to transect 120, transect 120, and Road R-1 connecting transects 120 and 121. On 21 October 1998, we added 21 additional traps along the road and in the area of HFBS transect 117, where translocated palila frequently roosted. During sessions 4 and 5, we placed carnivore traps at 1-km intervals along the major roads on the western slope. We also placed nine traps on both of the palila study grids (see Chapter 9: Breeding Phenology, Productivity, and Nesting Success). During sessions 6 and 7, we placed a total of 105 carnivore traps on the western slope. We placed traps along HFBS transects 101–103, 122–126, and 129 at 600-m intervals near existing HFBS stations. We also placed traps 600 m apart along the firebreak road at the lower boundary of Ka'ohe Game Management Area. We trapped during the palila breeding season (April–August; Table 36.1) to minimize the effects of carnivore predation on palila nests. During sessions 8 and 9, we placed traps in an array similar to that used in session 3. We placed 20 traps on HFBS transects 116–121 (stations 3, 7, 11, and 15, where present), 25 traps in the predator grid, and 17 traps along Road R-1, 0.5 km apart, between HFBS transects 121 and 118.

During 27 November 2004–17 February 2005 of session 9 we fitted 10 traps in the predator grid with telemetry transmitters (Benevides *et al.* 2008). During 1–17 March 2005 we fitted seven traps along transects 119 and 120 with telemetry transmitters. These traps transmitted a signal when open but did not transmit a signal when closed or tripped. This enabled us to check those traps with telemetry receivers and antennas from a distance. Nevertheless, we continued to check these traps daily, as this technology was in the experimental stage.

In 2003, an independent party also trapped cats and mongooses on the western slope. They placed 30 traps in an area north of R-14, south of the pasture, west of Road R-13, and east of Saddle Road.

For long carnivore trapping sessions (600 trap-nights or longer), we used linear regressions to compare the relationship between carnivore capture rates ($\log_{10}$ transformed) and time (binned by 150 trap-nights). We used the y-intercept as a measure of initial carnivore abundance in the effective trapping area. For mongooses, we examined only session 6 with a linear regression, as it was the only session over 600 trap-nights when poison baits (diphacinone) were not applied for rat control (see below). Mongooses are highly sensitive to diphacinone. In addition, for each session, we used the cat capture rate of the first 150 trap-nights to compare initial cat abundances.

During sessions 6–9, we determined the age and sex of animals based on their reproductive condition. We also collected and sent lower canine teeth from cats to Matson's Laboratory, L.L.C. (Milltown, MT) for cementum annuli aging (Danner *et al.* 2010). We collected blood samples to assess the prevalence of feline immunodeficiency virus, feline leukemia virus (FeLV), and the coccidian protozoan *Toxoplasma gondii* (Danner *et al.* 2007). Feline immune-deficiency virus and FeLV have been evaluated as potential biological control agents in island ecosystems (Courchamp and Sugihara 1999). We also collected pectoral muscle tissue samples and stored them in lysis buffer for population genetics studies (Hansen *et al.* 2007).

To test rodent control methods, we distributed poison bait on a 1-km^2 predator grid on the northern slope of Mauna Kea. The predator grid covered the core area of palila activity on the northern slope, consisting of 21 transects, spaced 50 m apart, each with 21 stations spaced 50 m apart, yielding 441 stations. All poison bait consisted of diphacinone (2-Diphenylacetyl-1, 3-Indandione). Prior to palila translocation 3 (T3), we placed Protecta® Tamper Resistant bait stations (28 x 28 x 15 cm), each with two Eaton® (EPA Registration No. 56-44) peanut butter/molasses or fish-flavored bait blocks (56 g each), at each station. Prior to translocation 4 (T4), we replaced some of the bait stations with Protecta® LP bait stations (34 x 23 x 9 cm) and placed four Ramik® (EPA Registration No. 61282-12) peanut butter-flavored mini-bar bait blocks (31 g each) in each station. During T4, we replaced diphacinone monthly during December 2003–May 2004 and then again during 19 September–1 December 2004. Due to a rodent irruption during T5, the diphacinone was consumed more rapidly than usual. This necessitated replacing diphacinone every several days in a reduced area of the predator grid (122,500 m^2, stations 0L–6T) during 10 December 2004–2 March 2005. We returned to monthly application during April–June 2005. All baits were handled and distributed according to their labels, special local need guidelines, and material safety data sheets.

Results

We captured feral cats and mongooses with canned cat food, sardines, and mackerel. Over 11,736 trap-nights, we captured 155 feral cats (Table 36.2). We captured cats between 2,150 and 2,950 m elevations, but we opportunistically collected cat scat as high as 3,064 m elevation. We recaptured cats from sessions 4 and 5 in session 6 ($n = 2$) and session 7 ($n = 3$). Although we typically captured very few juveniles, 26% of cats in session 7 were juveniles. We

Table 36.2. Date, location, effort, and capture rates of feral cats (*Felis catus*) by age and sex on Mauna Kea, Hawai'i, 1998–2005.

Session	Date	Slope	Trap-nights	Female		Male		Total	Cats/ 100 trap-nights
				Ad	Juv	Ad	Juv		
1	Apr–Jul 98	North	229	7	3	6	1	17	7.42
2	Jul–Aug 98	West	355	3	2	7	1	13	3.66
3	Sep 98–Mar 99	North	2,628	9	0	9	0	18	0.68
4[a]	Jun–Jul 1999	West	170	1	0	6	0	7	4.12
5[a]	Sep 00	West	281	3	0	5	0	8	2.85
6	Apr–Aug 02	West	3,130	6	2	12	0	20	0.64
7	Jun–Aug 03	West	651	6	6	17	2	31	4.77
8	Nov 03–May 04	North	2,128	12	0	8	1	21	0.99
9[b]	Nov 04–Jul 05	North	2,208	9	1	7	2	20	0.91
Total			11,780	56	14	77	7	155	

[a] Most feral cats were radio-tagged and released during these sessions. In session 4, we removed two and recaptured zero feral cats. In session 5, we released all animals, including seven recaptured feral cats from within this session (not included in this table), and recaptured five feral cats from session 4 (we captured five of these animals more than once in session 5, but we only included the first capture of session 5 in this table).

[b] We trapped 20 cats during session 9, but morphological data for one cat are missing.

trapped pregnant female cats in April of session 6 (*n* = 2), May of session 1 (*n* = 1), and November (*n* = 2) and February (*n* = 1) of session 9. We trapped lactating females in May of sessions 1 and 6 (*n* = 2), July of session 7 (*n* = 1), and April and June of session 9 (*n* = 2).

When we examined the five long trapping sessions (3, 6, 7, 8, 9), we found that cat capture rates on the northern slope decreased significantly in sessions 3 and 8 but increased significantly in session 9 (Table 36.3, Figure 36.2). Capture rates did not change on the western slope in sessions 6 or 7 (Figure 36.3). The inverse $\log_{10}$ of the y-intercept yielded an estimate of initial cat abundance within the effective trapping area for each session (Table 36.3). In all five cases, these estimates were less than the number of cats that we removed during the session. Although the number of cats caught in the initial 150 trap-nights ranged from three to eight cats (Figures 36.2, 36.3), we always caught fewer cats in the following 150 trap-nights.

In addition to our trapping effort on the western slope in session 7, an independent party captured 25 cats and 8 mongooses in approximately 3,600 trap-nights between late April and late August 2003.

Over 11,736 trap-nights, we captured 128 mongooses (Table 36.4). We caught mongooses between 2,200 and 2,850 m elevations. Overall, mongooses were trapped less often than feral cats on Mauna Kea, with fewer mongooses caught in six of nine trapping sessions. Mongooses were the more abundant carnivore in sessions 2, 6, and 9. In session 8, we caught three mongooses in the predator grid before diphacinone application (388 trap-nights over 37 calendar nights) and none after diphacinone application (961 trap-nights over 158 calendar nights). Although we typically trapped few juveniles, 7 of 39 (18%) mongooses from session 6

Table 36.3. Session, slope, linear regression results, and estimated initial abundance of animals per effective trapping area for carnivore trapping sessions 3, 6, 7, 8, and 9 on Mauna Kea, Hawai'i.

Session	Slope	Regression equation	r^2	*P*	Estimated initial abundance†
Feral cat					
3	North	y = -0.0002x + 0.4805	0.33	0.015	3.0
8	North	y = -0.0004x + 0.7068	0.66	<0.001	4.7
9	North	y = 0.0002x + 0.0615	0.31	0.038	1.2
6	West	y = -0.0001x + 0.3946	0.12	0.145	9.4
7	West	y = -0.0001x + 0.9744	0.14	0.622	2.5
Mongoose					
6	West	y = -0.0002x + 0.7111	0.55	<0.001	5.1

†Estimated initial abundance was taken from the y-intercept of the linear regression.

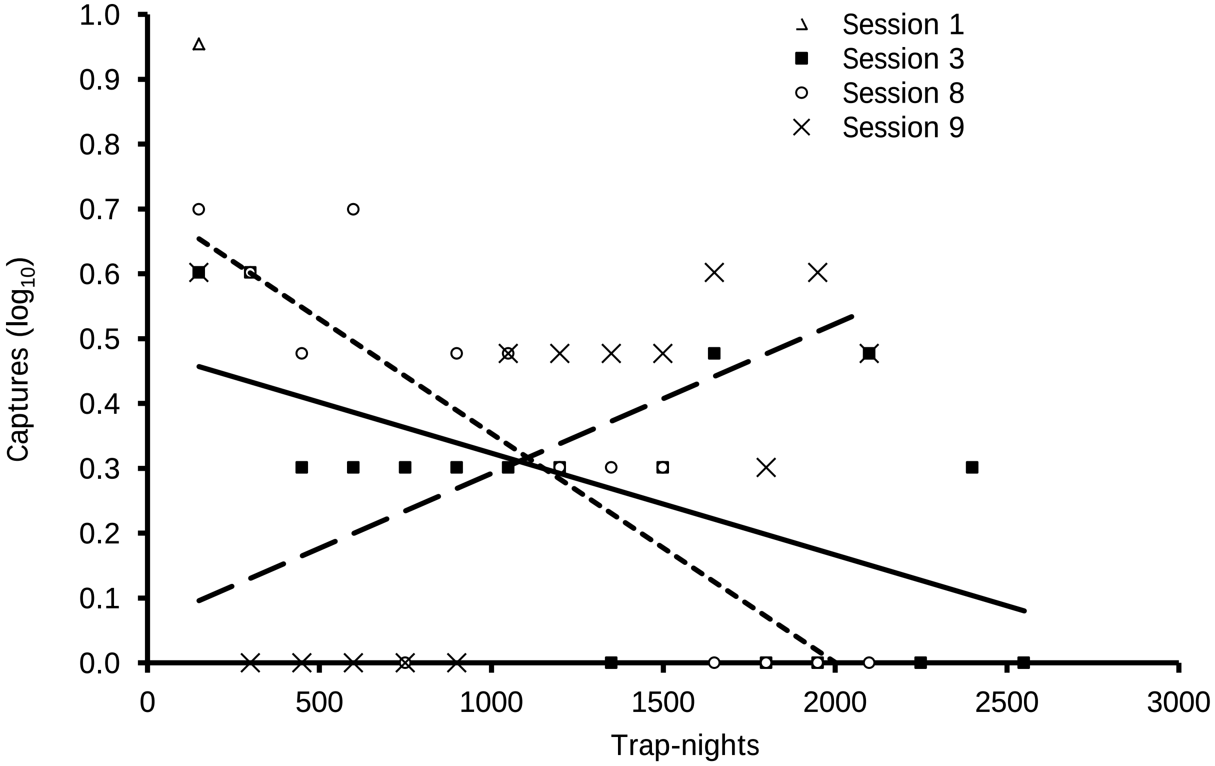

Figure 36.2. Relationships between the $\log_{10}$ of feral cat captures and time (binned at 150 trap-nights) from four sessions on the northern slope of Mauna Kea, Hawai'i, 1998–2005. Regressions were calculated only for the three sessions having >600 trap-nights.

were juveniles. We trapped five of these juveniles in May, one in June, and one in July. We trapped pregnant females in April (n = 4), May (n = 1), and August (n = 1) of session 6; July of session 7 (n = 1); and December (n = 1) and March (n = 1) of session 9. We trapped lactating females in April of session 8 (n = 1), July of session 7 (n = 6), and August of session 2 (n = 1).

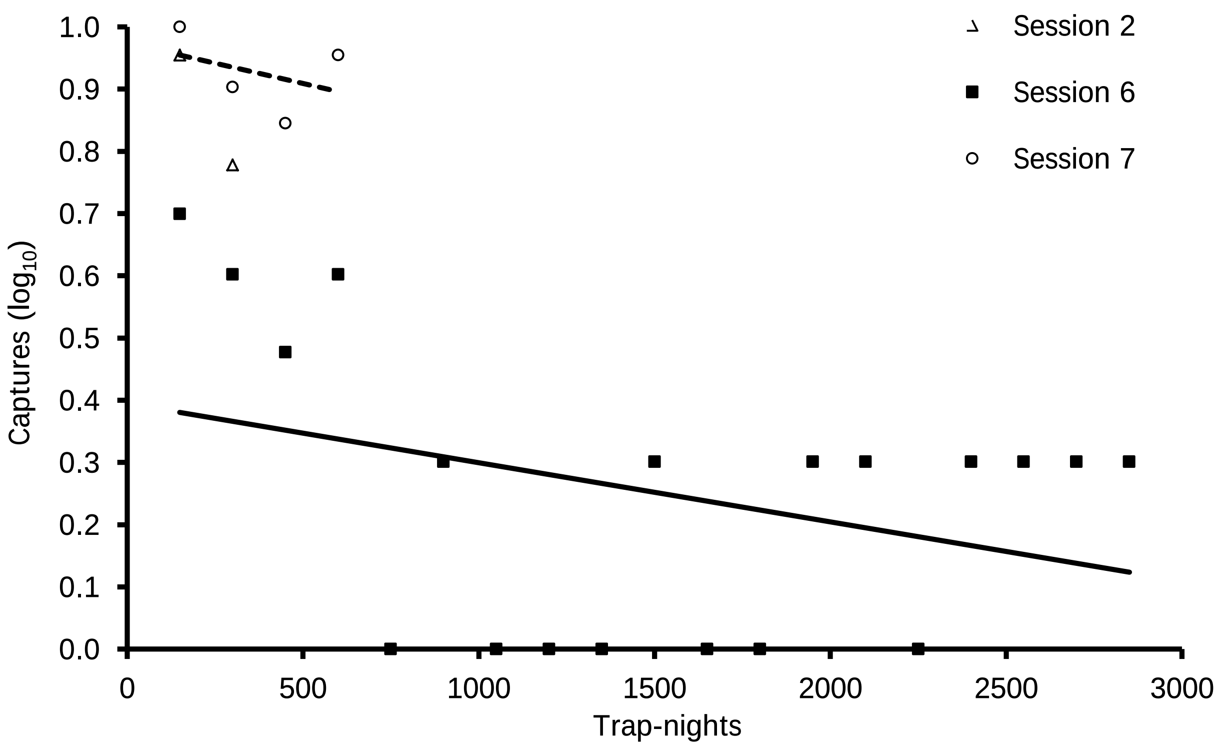

Figure 36.3. Relationships between the $\log_{10}$ of feral cat captures and time (binned at 150 trap-nights) from three sessions on the western slope of Mauna Kea, Hawai'i, 1998–2003. Regressions were calculated only for the two sessions having >600 trap-nights. Sessions 4 and 5 are not included because they were catch/release sessions.

Table 36.4. Date, slope, effort, and capture rates of mongooses (Mong; *Herpestes auropunctatus*) by age and sex on Mauna Kea, Hawai'i, 1998–2005.

Session	Date	Slope	Trap-nights	Female		Male		Total	Mong/ 100 trap-nights
				Ad	Juv	Ad	Juv		
1[a]	Apr–Jul 98	North	229	1	0	3	0	5	2.18
2	Jul–Aug 98	West	355	7	0	7	0	14	3.94
3	Sep 98–Mar 99	North	2,628	5	0	5	0	10	0.38
4[b]	Jun–Jul 1999	West	170	–	–	–	–	3	1.76
5[b]	Sep 00	West	281	–	–	–	–	6	2.13
6[c]	Apr–Aug 02	West	3,130	10	5	21	2	39	1.25
7	Jun–Aug 03	West	651	6	0	8	0	14	2.15
8	Nov 03–May 04	North	2,128	3	1	5	1	10	0.47
9	Nov 04–Jul 05	North	2,208	4	0	20	3	27	1.22
Total			11,780	36	6	69	6	128	

[a] No age/sex data collected for one mongoose during session 1.

[b] No age/sex data collected for mongooses during sessions 4 and 5.

[c] One female of unknown age captured during session 6.

One of the lactating females in session 7 was accompanied by a juvenile that escaped from the trap.

We found that mongoose capture rates decreased significantly as cumulative trap-nights increased in session 6 (Table 36.3). For session 6, the inverse $\log_{10}$ of the y-intercept yielded an initial mongoose abundance estimate of 5.1 mongooses for the trapping area, representing only 13% of the number actually captured.

Eaton and Ramik diphacinone bait blocks were distributed primarily to protect palila that were reintroduced to the northern slope of Mauna Kea. We were unable to measure the change in rodent numbers due to this management action. Nevertheless, we observed feces of rats, mice, and mongooses in the bait boxes and we saw tracks of mongooses outside of the entrances to bait boxes. In 2004, we found two dead mice and one lethargic mouse that were presumably poisoned from eating diphacinone outside of bait boxes in the predator grid. During session 9, numerous dead mice were found inside bait boxes.

Discussion

Overall capture rates for feral cats during our study were similar to capture rates recorded during other studies on Mauna Kea, although our capture rates ranged from 0.64–7.42 per session (Table 36.5). The wide range in capture rates may partly reflect environmental variability in subalpine Mauna Kea over six to eight years of trapping effort. Additionally, changes in the cat population through attrition (by trapping), reproduction, and environmental factors such as prey availability, may have affected capture rates among sessions.

Table 36.5. Capture rates of feral cats and mongooses (Mong) on Mauna Kea, Hawai'i.

Study	Slope	Date	Trap-nights	Cats/100 trap-nights	Mong/100 trap-nights
van Riper (1978)	West	1973–1975	969	1.86	3.51
U.S. Geological Survey[1]	West	1992	250	2.0	–
U.S. Geological Survey[1]	North	1992	167	2.3	–
this study	West	1998–2003	4,587	1.72	1.66
this study	North	1998–2005	7,193	1.06	0.72

[1] Unpublished data (S. G. Fancy *et al.*)

Controlling the feral cat population on Mauna Kea may not require continual, high-intensity trapping as we found that many cats were removed during the initial 1,000 trap-nights. Feral cat capture rates declined significantly during sessions 3 and 8 and non-significantly during sessions 6 and 7. After decreasing, the capture rates during the longer trapping sessions stabilized at a lower level, suggesting immigration from surrounding areas after the removal of all resident cats. Nevertheless, cat capture rates increased significantly in session 9. The beginning of session 9 trapping coincided with a rodent irruption on Mauna Kea (see Chapter 33: Rodent Survey), and the overabundance of prey may have made our baits less attractive initially. Moreover, the abundance of food may have increased cat survival, reproduction, and immigration, potentially increasing the number of cats available to be trapped later in the session. Because cat trapping may be an ineffective control method during rodent irruptions, the availability of natural prey should be considered before beginning a trapping program.

Interruptions between and during our trapping sessions suggest that breaks of up to two months did not affect the subsequent cat capture rate. On the northern slope, a trapping break of less than two months occurred between sessions 1 and 3, and during session 8 we stopped trapping for about one month (25 Jan–3 Mar 2004) after the initial 1,101 trap-nights. The cat capture rates did not increase after these breaks, suggesting only limited immigration after one or two months. On the other hand, long breaks in trapping were followed by higher capture rates, as we observed on the western slope during the initial 150 trap-nights of session 7, which began 10 months after the conclusion of session 6. The high cat capture rate and high percentage of juveniles captured during session 7 (July and August) may have been due to juvenile dispersal from the surrounding areas. Alternatively, prey availability, which strongly influences cat home range size (Edwards *et al*. 2001), may have accounted for the increased capture rate. Session 7 occurred during a dry year when rodent populations were relatively low (Chapter 33: Rodent Survey), possibly increasing the attractiveness of our baits.

Our estimated initial abundance of carnivores was always lower than the actual number of cats removed during that session. This may have been an artifact of our circulating trapping effort. Approximately 600 trap-nights were required to cover the entire trapping area. Therefore, we would not expect to capture all resident cats until we had trapped throughout the entire area. Immigration could also have affected capture rates, as may have occurred in session 6.

In sessions 6 and 7, we recaptured two and three cats, respectively, that were trapped and released in sessions 4 and 5. The recapture of these released cats required several thousand trap-nights, two to four years after their initial capture, suggesting that these cats may have become “trap shy.” Alternative trapping techniques may be necessary for removing trap-shy cats.

Although our overall mongoose capture rate was lower than that of van Riper (1978; Table 36.5), his result was bracketed by the range of our capture rates per session (0.38–3.94). We found that mongooses bred primarily in the summer months but also bred during the winter. Therefore, we expected the majority of juvenile dispersal to occur in the late summer or fall. Nevertheless, trapping data from session 6 suggested that juveniles were more abundant during May–July. Mongoose capture rates decreased significantly during the only long session without diphacinone application (session 6). Even so, we still captured animals regularly up to about 2,000 trap-nights during session 6. Current carnivore trap arrays are spaced according to cat movement data, and our results suggest that closer trap spacing may be more effective for mongoose control. In addition, very young mongooses were able to escape from our live traps. The lack of mongoose captures in the predator grid after diphacinone application suggested that poison bait was effective for mongoose management. Intensive poison baiting on a larger grid before reintroducing palila to an area, during the nesting season, and during mongoose dispersal may be the most effective methods for protecting palila from mongooses (Hays 1999).

Rats and mice entered diphacinone bait boxes and consumed bait. Although we did not evaluate changes in rodent populations before and after distributing diphacinone, we observed dead mice at the bait stations. Although poison-killed rodents might pose a potential hazard for ʽio (*Buteo solitarius*) and other raptors, results of other studies suggest that rats tend to die underground or in other inaccessible locations, thus minimizing threats (Lindsey and Mosher 1994, Spurr *et al*. 2003). Secondary poisoning is even less likely to occur due to the low number of poisoned rodents we found outside bait stations and the small number of ʽio we saw or that were reported (Scott *et al*. 1986, Klavitter 2000) in subalpine Mauna Kea. Because we distributed the baits in strict accordance with label instructions (EPA Registration No. 56-44 and No. 61282-12), there was little risk of secondary or incidental poisoning to non-target organisms (Hacco 2003, JT Eaton 2004).

Palila experience less predation when measures are taken to reduce populations of small introduced mammals. During the 1999–2001 palila nesting seasons, when there was no predator control on the western slope, feral cats depredated 8–11% of active nests annually (see Chapter 9: Breeding Phenology, Productivity, and Nesting Success). In contrast, we observed no nest predation by cats during the 2002 breeding season, when we trapped intensively. Additionally, we did not control small mammal numbers during the second translocation trial, and we implicated rats in the deaths of two palila and the deaths or scavenging of three others (see Chapter 2: Translocating Wild Palila). Predation decreased markedly during the third, fourth, and fifth translocation trials.

This study demonstrated that removing small introduced mammals can be effective in reducing predatory threats to the palila and other native birds on Mauna Kea. Our trapping program also led to practical information about the population genetics, demography, diseases, and habitat relationships of feral cat populations in Hawai'i (Hess *et al*. 2007a). The genetic structure of feral cats in Hawai'i indicates great dispersal ability between the slopes of Mauna Kea and even between the volcanoes of Hawai'i Island (Hansen *et al.* 2007). This suggests that control will be difficult due to high rates of immigration as cats are removed from areas. Moreover, high rates of reproduction and survival can be supported by abundant bird prey, and male cats may be limited more by the availability of mates than of food (Hess *et al.* 2007b). Relatively high survival (to 11 years of age) and reproduction also allow individual cats to affect palila for many years and enable cat populations to recover quickly after control efforts (Danner *et al.* 2010). Feline immunodeficiency virus, feline leukemia virus, and *Toxoplasma gondii* may depress the feral cat population on Mauna Kea to some degree, but their occurrence suggests they would not be effective agents in a biological control strategy (Danner *et al.* 2010). Cats were captured more often on the western slope and in māmane (*Sophora chrysophylla*) woodland (Hess *et al.* 2007a), and increasing control efforts near sites of multiple captures may prove more effective than trapping uniformly across the landscape. The number of mongooses captured at a trap was positively correlated to the number of cat captures even though mongooses pre-empted traps; therefore, using alternate control measures, such as diphacinone, might increase the rate of cat captures (Hess *et al.* 2007a). Our extensive research on feral cats and other introduced small mammals on Mauna Kea provides additional information that can be used in an adaptive management framework to improve the effectiveness of predator control to protect palila (Hess *et al.* 2007a, 2009).

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SECTION VI: MANAGEMENT IMPLICATIONS

Preface

Our research is intended to provide information that can be applied to the conservation of the palila and restoration of its habitat. Some of our results are expected to have immediate, practical value; whereas, other information is more likely to aid managers by helping them understand the species and system they are working to protect. A broad knowledge of the ecology of the palila and its environment are important for evaluating the results of management actions and for developing new conservation strategies as conditions change. We also hope that our work will help increase the general public’s knowledge of the palila and Hawai‘i’s natural heritage. In Chapter 37, we discuss how our results are relevant to palila recovery.

37 IMPLICATIONS OF RESEARCH FOR PALILA RESTORATION

Paul C. Banko, Chris Farmer

Introduction

The history of research into the conservation biology of the endangered palila (*Loxioides bailleui*) extends over four decades with many biologists dedicating years of effort to understanding this species. As a result, more is known about the palila's ecology and its conservation needs than any other Hawaiian bird. It is especially important, therefore, to apply this rich and extensive ecological knowledge of the species to its recovery. In the following, we highlight information that is most relevant to palila recovery.

Population Reintroduction and Restoration

Evaluating Sites for Reintroduction

As indicated in the most recent recovery plan for Hawaiian forest birds (U.S. Fish and Wildlife Service 2006), palila are at risk of extinction primarily because they are concentrated in a small area of māmane (*Sophora chrysophylla*) forest on the western slope of Mauna Kea. The plan identified habitat degradation due to browsing by introduced ungulates and the high risk of fire as key factors threatening the palila. In addition to protecting the existing population, the plan highlighted the need to reestablish palila in multiple locations within its historical range. With this goal in mind, we evaluated three sites on Mauna Kea and one site on Mauna Loa for their potential to support an experimental reintroduction of palila.

Our surveys revealed extensive habitat damage by browsing ungulates and the widespread distribution of fire-promoting alien grasses and other fine fuels. Nevertheless, we also discovered that māmane has been recovering to a limited degree on Mauna Kea due to annual culling of ungulate populations by public hunting and aerial shooting since 1980. On Mauna Loa at Kīpuka ʻAlalā in Pōhakuloa Training Area, we found little recruitment of māmane, although naio (*Myoporum sandwicense*) and ʻaʻaliʻi (*Dodonaea viscosa*) were thriving despite the presence of ungulates. Casual inspection of the Kīpuka ʻAlalā study site indicated substantial māmane regeneration following the removal of ungulates, suggesting that habitat conditions might eventually improve sufficiently to allow the reintroduction of palila.

Māmane food resources were available throughout the year where the habitat was distributed along a broad elevation gradient. Moreover, the large expanse of māmane forest extending along a broad elevation gradient on the western slope of Mauna Kea was a key factor contributing to the concentration of palila there (Scott *et al.* 1984, Banko *et al.* 2002a). Palila populations can be reestablished more readily where there is high potential for expanding māmane forest size, density, and altitudinal range following the removal of browsing ungulates.

Our surveys indicated that the southern slope of Mauna Kea had high potential for supporting palila due to its relatively high density of māmane trees and saplings. The southern slope and the adjacent Pōhakuloa Flats area together composed a large expanse of forest and supported substantial gradients of elevation and rainfall, which potentially would provide food to palila throughout the year. Nevertheless, ongoing military activity and highway development could impede palila recovery in the southern portion of Palila Critical Habitat (PCH), where palila have become extremely rare.

Alternatively, we found that the northern slope offered a suitable and immediate option for reintroducing palila. The main attraction of the northern slope was the potential, now underway, for eliminating ungulates and restoring māmane forests on pasturelands below PCH. Extending the gradient of elevation over which palila can track māmane pods while improving habitat quality throughout the area would provide support for a critical second population in the event of a catastrophe within the core habitat of the palila on the western slope.

Despite the limited range of elevation and size of the forest at Kīpuka ʽAlalā (1200 ha), habitat restoration there could be accelerated by planting seedlings or scattering seeds of māmane, as is being done on the northern slope of Mauna Kea by the Mauna Kea Forest Restoration Project (R. Stephens, personal communication) and in montane habitat on Mauna Loa in Hawaiʽi Volcanoes National Park (S. McDaniel, personal communication). By itself, Kīpuka ʽAlalā may never support many palila without intensive management, but it could play an important role in recovery if palila are eventually reintroduced to the western slope of Mauna Loa (Banko *et al.* 2009).

Translocating Wild Palila

From our six translocation trials, we developed methods that resulted in the high survival of birds and the establishment of a small, breeding colony. The highlight of the project was the production of many first-generation palila and at least one second-generation palila at the site. Another milestone was discovering that some translocated birds periodically moved between the reintroduction site on the northern slope of Mauna Kea and the source site on the western slope, and unbanded birds regularly were detected on the northern slope. Movement between slopes would be an important means of connecting the populations and might eventually lead to palila moving between habitats according to the condition of the vegetation, availability of food, and other environmental factors.

The greatest problem we encountered was the low persistence rate of birds at the reintroduction site. Although some birds remained for over a year, many returned to their point of origin on the western slope within two months. We were unable to predict which individuals were likely to remain and breed in the reintroduction area. The return of translocated birds to the source area was partially offset by palila that moved between the northern and western slopes.

Ultimately, the reintroduced colony disappeared due to severe drought conditions and the lack of sufficient resources for augmenting the colony with additional birds. We were unable to determine whether birds that had bred on the northern slope eventually returned to the western slope or died. Palila that were fledged on the northern slope generally remained there longer than their parents, based on sightings of birds in the years following the last translocation in 2006. Severe drought conditions prevailed during most of the study, and its effect on the translocation results are not clear. Nevertheless, the effects of drought on māmane trees seemed somewhat less severe on the northern slope than they were on the western slope, suggesting that additional translocation efforts coupled with increased habitat restoration could result in a more enduring population.

Despite the relatively high potential of the northern slope for reestablishing a palila population, patterns of habitat use by the translocated birds revealed the marginal value of large areas of habitat where māmane cover was sparse. Translocated birds concentrated in two habitat patches where the size and density of māmane trees were highest and spent relatively little time elsewhere. Therefore, habitat restoration to improve the carrying capacity for palila is necessary for reestablishing a population on the northern slope. The most effective methods of promoting habitat recovery are to remove ungulates permanently from PCH and increase māmane cover through planting and other means where natural regeneration is poor.

Protecting translocated palila from predators was important to reduce mortality in the reintroduction area. Palila were selective about the location and species of tree they used for roosting after being translocated. This, in addition to their initial lack of familiarity with the new area, may have increased their vulnerability to predation from introduced mammals and native raptors. Predation of even a few individuals would have a disproportional impact on the overall survival and productivity of a small population.

Harvesting Wild Eggs and Supplementing Food at Nests

A potential tool for bolstering wild populations is rear-and-release, which involves harvesting wild eggs for propagation in captivity and releasing the young birds to the wild (Lieberman and Kuehler 2009). This method of producing birds to augment or reintroduce populations in the wild might be feasible, even if with substantial effort, because wild palila nests are not particularly cryptic or difficult to access compared with nests in taller, denser forests. Moreover, we found that palila readily re-nested after their eggs were removed for artificial incubation. Nevertheless, in years of severe drought, which have occurred frequently in recent years, relatively few palila nested due to the scarcity of māmane pods (Banko *et al.* 2013). Although rear-and-release might be practical only in years when conditions were favorable for breeding by wild pairs, our work suggests it may be ineffective to release captive-reared birds or translocate wild birds under harsh environmental conditions, when poor survival would be expected.

We attempted to supplement the diet of wild palila nestlings but found it to be logistically impractical. Opportunities to directly supplement the diet of nestlings were infrequent because females were away from the nest on only a few occasions each hour, and recesses generally lasted fewer than 10 minutes. We also failed to attract nesting adults to supplemental foods. Pairs ignored food items placed near the nest, probably because they seldom or never foraged in the nest tree during chick rearing. Placing supplemental food away from nest trees in areas where adults frequently forage may yield more promising results. Supplemental feeding trials might also be more productive in naio-dominant forest, where māmane food resources are less available. Given that much more work is needed, supplemental feeding as a management tool for sustaining palila during nesting or times of food shortage does not seem promising in the near-term. Before investing more effort in developing supplemental feeding techniques, it would be helpful to evaluate the effects of diet augmentation and the effect of different diets on the growth of palila nestlings. Nevertheless, improving habitat quality throughout PCH would undoubtedly increase palila survival and reproduction.

Release and Monitoring of Captive-reared Palila

The staff at Keauhou Bird Conservation Center was successful in propagating and releasing a limited number of palila on the northern slope of Mauna Kea (Lieberman and Kuehler 2009). Although many birds disappeared within two months, one captive-reared male survived on the northern slope of Mauna Kea for seven years. Captive-reared females were not known to have produced chicks, but at least two males nested successfully with translocated females or their progeny.

We noticed differences in foraging behavior and song structure between some captive-reared and wild palila. Measures to reduce behavioral differences through conditioning or parent-rearing might result in increased survival and breeding after release to the wild. Even so, difficulties in producing larger numbers of palila in captivity will need to be overcome before captive propagation is likely to play a significant role in reintroducing palila to former range or bolstering the existing population. Neither wild birds that were brought into captivity nor birds that were reared in captivity from wild-harvested eggs have bred readily.

Demography and Breeding Ecology

Population Trends and Response to Environmental Factors

Annual population surveys revealed that the palila population declined significantly after 2003, primarily due to severe drought conditions and continued habitat degradation by browsing ungulates (Banko *et al*. 2013). Between 1998 and 2012, the population estimate reached a maximum of 6,463 in 2003 and a minimum of 1,495 in 2011 for an average loss of over 500 birds annually. The rate of decline was 57% over the 15-year period (Camp and Banko 2012). During this time, the range of the palila also contracted, increasing the vulnerability of the species to environmental disturbance and invasive species threats (Banko *et al.* 2013).

Drought was largely responsible for the decline in palila numbers and range because of its strong effect on māmane pod production, which in turn affects palila survival and reproduction (Banko *et al*. 2013). Despite the effects of drought on pod production, habitat carrying capacity could be substantially improved for palila by eliminating browsing ungulates, planting māmane and other native trees and shrubs in areas with sparse regeneration, and possibly reducing the cover of invasive grasses and other weeds that may compete with native plants (Banko *et al*. 2013).

Given the magnitude of the palila's decline, it is important to continue to improve the annual population survey. One method for improving the precision of the annual counts is to sample the survey stations more than once, thereby increasing the numbers of detections, reducing the total uncertainty in the abundance estimates, and improving the overall power to detect population changes (Camp and Banko 2012). In addition, repeat surveys allow for state-space modeling, which can be used to identify observation and process error in the population estimates. Process error is the inherent uncertainty in estimating the population due to temporal and spatial variability and natural population fluctuations. Observation error is associated with sampling, detecting birds, and population modeling. Reducing observation error will allow a more precise accounting of the process error (noise) in the population estimates.

Sex Ratio

Both genetic (PCR) and plumage techniques for sexing palila indicated a significant difference in sex ratios among age classes. There was a strong tendency towards males in the adult age class (after second year or ASY) where males outnumbered females by 50% or more in both sample types. The sex ratio changed to a male bias after individuals began breeding. Both methods of sex determination indicated parallel shifts in sex ratios from hatch year (HY; tendency towards more males) to second year (SY; female bias) to ASY (male bias) as Lindsey *et al.* (1995) reported. We found that sexing SY birds using the plumage-based technique alone was subject to a high error rate; but even when corrected the results were female-biased.

Determining the sex ratio and how it may change between age classes is important for calculating survival rates, conducting population viability analyses, and planning conservation strategies for endangered species. As the palila population declines, the effects of the male-biased sex ratio may become increasingly problematic due to increased demographic stochasticity and competition for mates.

Disease

Avian malaria is unlikely to affect the existing palila population or future reintroduced populations in subalpine Mauna Kea, where mosquitoes and other vectors are absent or rare (Banko *et al.* 2009). We rarely observed lesions caused by avian pox virus in palila, although lesions were encountered more frequently in bird species that seasonally vacated the lower-elevation, wetter forests of windward Mauna Kea to feed on māmane flowers within the palila's range (Hess *et al.* 2001). Despite proximity to pox- and malaria-infected birds, the lack of an effective vector protects the palila in the near-term. Although changes in climate could eventually increase the exposure of palila to disease vectors, the recent trend towards drier conditions in subalpine Mauna Kea (Banko *et al.* 2013) is not likely to favor mosquitoes. Nevertheless, additional screening for avian diseases and vectors is warranted within Pōhakuloa Training Area (see Figure I.1) and other potential reintroduction sites at relatively low elevations. The occurrence of mosquitoes within PCH could be detected and managed with periodic monitoring. The effects of bacterial diseases and other pathogens are of concern for successful palila management because of their possible implication in the deaths of captive chicks. *Mycoplasma* bacteria have not been cultured from wild palila or other honeycreepers within PCH.

Breeding Demography

Although palila live and breed to at least 17 years of age (Banko *et al.* 2013), we found during 1999−2002 that the mean breeding age varied annually between 4.2 and 6.1 years; almost 20% of nesting adults were older than 6 years, and a few adults older than 10 years were breeding each year. Breeding palila were significantly older than birds not associated with nests, due mainly to a greater proportion of 9–10-year-old birds in the breeding population. Although we did not determine whether older parents had higher fledgling success rates, it is likely that experienced adults formed a larger proportion of the breeding population in years when food availability was marginal than when it was abundant. Increasing the carrying capacity of the habitat should provide younger palila with more opportunities for breeding and breeding activity should increase annually among all pairs.

In agreement with Pratt *et al.* (1997), we found that palila nested in the same general area each year. Assuming that nest location was influenced mainly by the distribution of food or prior nest success, increasing the density of māmane trees around nesting sites might boost the breeding frequency and nesting success of individual pairs. Similarly, enhancing habitat quality where palila nesting density is low should attract new breeding pairs. Although Fancy *et al.* (1993) reported limited dispersal by palila, we found that the nests of some palila were separated by more than 1.7 km from year to year. This suggests that palila should readily colonize restored habitat adjacent to or near their core range.

Genetic studies indicated that males may gain nesting experience by helping at the nests of parents or close relatives (Patch-Highfill 2008), which likely increases nesting success and reduces the overall costs of nesting (Miller 1998). Nest helping by males may increase if the sex ratio becomes increasingly male-biased.

Breeding Phenology, Productivity, and Nesting Success

Palila nesting activity varied considerably in timing and in terms of the number of pairs breeding from year to year, presumably mostly in response to food availability (Pratt *et al.* 1997, Banko *et al.* 2002a, Banko *et al.* 2009). We found a positive correlation between the number of active nests during the breeding season and the number of māmane pods available. For example, the number of pods per tree was higher in the spring of 2002 than in the previous three years, which may partly explain the peak of palila numbers in early 2003 (Banko *et al.* 2013). The ability of palila to nest vigorously in some years may help offset drought years with poor productivity (Lindsey *et al*. 1997, Banko *et al.* 2013).

We found that nest density was usually higher in māmane-dominated forest than it was in naio-dominated forest, although the naio habitat encompassed a large area of the western slope and supported many nesting pairs, at least in some years. Māmane-dominant forest was distributed at a higher elevation, making māmane seeds available earlier in the season (Banko *et al*. 2002a). More palila should nest in the lower elevation forest, which is now dominated by naio, as māmane regeneration continues to outpace naio regeneration there (Hess *et al.* 1999), and the trend toward more māmane will accelerate once browsing ungulates have been eliminated. Other measures of improving habitat to encourage nesting in naio-dominated areas would be planting māmane and reducing the cover of invasive grasses and other weeds.

The availability of food during the breeding season may also affect nest success, although further research is needed to understand the underlying mechanisms and interactions among variables. We found that 33–67% of palila nests were successful annually during 1996–2004 (excluding 2001), which was similar to the range (39–55%) reported by Pratt *et al*. (1997) during 1989–1993. Nevertheless, palila nestlings are potentially vulnerable to predators and storms for 21–30 days (van Riper 1980a, Pletschet and Kelly 1990, Banko *et al.* 2002b). Reducing predation increased nesting success. Feral cats (*Felis catus*) were responsible for many nest failures annually (Laut *et al.* 2003, Hess *et al.* 2004), but intensive trapping alleviated the problem. Reducing feral cat populations will be critical to the persistence and growth of small subpopulations of palila, and it could facilitate the spread of larger populations into marginal but recovering habitats. Nevertheless, some nests were depredated by native raptors, specifically pueo (*Asio flammeus sandwichensis*). An investigation of raptor ecology within the range of the palila could help determine their level of impact.

Nest Site Selection

Our model identifying the important vegetation characteristics associated with palila nest success identified the native mint, *Stenogyne microphylla*, as an important factor. The additional foliage of *S. microphylla* may have added important protection to nests, especially when māmane foliage may have been sparse due to drought. Palila also eat the buds, flowers, and young leaves of *S. microphylla*, which may have been important alternate foods in years of low māmane pod production.

Trees selected by palila for nesting during 1999−2004 were larger and taller than those in Pletschet and Kelly's (1990) study, suggesting that palila select larger trees when they are available. Large māmane will become more common on Mauna Kea as the young cohort of trees (Banko *et al*. 2009) continues to grow. To the extent that the growth of young trees is slowed by browsing, there should be faster growth and a greater number of preferred nest sites after ungulates are eliminated from PCH.

Palila nested primarily in māmane trees, but about 10% of nests were placed in other trees or shrubs, and one was placed in a grass clump. This variety of nesting sites suggests that palila may have used a much wider range of nesting sites before the composition of the forest was altered by ungulate browsing. Rats (*Rattus rattus*) might also affect the range of nest sites. For example, we never found a nest in ʻiliahi (*Santalum paniculatum*), which may be a species preferred by rats for foraging. Additionally, the amount of canopy overlap with neighboring trees was negatively associated with nest success, possibly because branches of neighboring trees increase the number of routes available to nest predators, such as rats and cats. Even so, we found that nest success also decreased as distance to nearest neighbor trees increased, suggesting that adjacent trees can provide additional cover from adverse weather and may help hide nests from aerial predators, such as owls. These results contrast with Pletschet and Kelly (1990), who found that nest trees isolated from neighboring trees proved to be more successful. The optimal amount of foliage overlap may change between years, depending on the different trade-off between cover and predation risk in any particular year. Our results suggest that reducing the risk of predation would result in palila nesting more frequently in denser tree cover, and tree cover will increase after browsers are eliminated (Scowcroft and Conrad 1988, 1992; Hess *et al.* 1999; Reddy *et al.* 2012).

Behavior at Nests

Only females incubated eggs and brooded nestlings. During the pre-fledgling stages, female palila were most attentive during the egg stage, presumably due to the embryo's greater sensitivity to changes in temperature than nestlings and the male's ability to provision the female more frequently before eggs hatch (Laut *et al*. 2003). Nest attendance decreased during the nestling period with break length increasing greatly over time as chicks became more covered with feathers and capable of thermoregulation (van Riper 1980a). We observed no evidence of heat stress in the behavior of females or nestlings. The need to simultaneously brood chicks and supply food explains why females recessed more frequently but for shorter periods during the early nestling period.

In our study, the average number of adult feeding visits did not change as nestlings aged, but Pletschet and Kelly (1990) reported that rates of feeding decreased later in the nestling stage. Our data were collected continuously and were less likely than theirs to misinterpret nest visits as feeding events. The growth rate of palila nestlings is slower than that for passerines of similar mass, which is probably due to their low rate of provisioning, specialized diet, and evolutionarily low risk of predation (van Riper 1980a, Laut *et al.* 2003, Banko and Banko 2009).

The long nesting period of palila makes them especially vulnerable to introduced mammalian predators. Predator control is important for palila recovery. Nest monitoring can be an effective method of evaluating predator removal programs. Video surveillance can identify predators at nests as well as document other factors contributing to nest failure.

Habitat Use and Food Ecology

Habitat Use, Home Range, and Movements

Understanding how palila interact with their habitat is critical to palila recovery. Although we found no significant differences between the home range sizes of translocated and non-translocated birds, translocated birds' daily movements were smaller than non-translocated birds. This suggests that there are differences between the quantity or quality of habitats on the northern and western slopes of Mauna Kea that influence palila habitat use. Mature māmane stands and mixed māmane-naio woodlands were less abundant on the northern slope, possibly influencing the persistence time of translocated palila.

We determined that the habitat selected for nighttime roost sites differed from that of daytime use areas. Mixed māmane-naio woodlands were important to palila for night roosting, probably because the dense canopy provided abundant cover. Maintaining sufficient night roosting cover could improve the success of translocations and releases of captive-reared birds.

Previously, palila were not known to move far around Mauna Kea (Banko *et al*. 2002b), but we found that palila were more mobile than previously suspected. We observed that translocated palila travelled between the northern and western slopes over a distance of up to 16 km. Nevertheless, radio-tagged, commuting palila were not detected between the two slopes, suggesting that palila moved rapidly and without using the habitat between the slopes. Restoring habitat between the two slopes might encourage the movement of palila and connectivity of reintroduced populations around the mountain. We also found that palila translocated to the northern slope used two distinct patches of māmane habitat that were separated by about 3 km of shrub habitat. Focusing resources on restoring and enlarging patches of current habitat might allow palila to persist among multiple sites until habitat can be restored across the wider landscape.

Habitat Use and Foraging Patterns

Palila habitat use is strongly influenced by the distribution and phenology of māmane, the seeds of which constitute the main portion of the diet (Banko *et al.* 2002a,b). Palila consumed reproductive parts and foliage of māmane, but took a higher proportion of māmane pods than other māmane food items relative to their availability. Palila spend proportionally more time in māmane trees and use māmane foods in much greater proportion to their availability compared to other foods. In mixed naio-māmane woodland, where naio density was greater than māmane density, palila spent more than twice as much time in māmane trees. Palila densities were related to pod availability and were higher in māmane woodland than in mixed woodland where māmane density was lower (Hess *et al.* 2001). Palila demonstrated limited ability to exploit alternate food resources, using naio fruits only occasionally and when māmane resources were scarce (Hess *et al.* 2001). Although palila consumed more flowers than pods in mixed woodland, they spent more time foraging on pods than other food items in both woodland types. Caterpillars were also consumed by palila and were taken mainly from inside māmane pods (Banko *et al.* 2002b).

The importance of māmane seeds in relation to movement, breeding, and survival of palila has been well documented (van Riper 1978, 1980a; Scott *et al.* 1984; Fancy *et al.* 1993; Lindsey *et al.* 1995; Hess *et al*. 2001; Banko *et al.* 2009, 2013). The nutritional value of seeds is high (Banko *et al.* 2002c) and contributes the largest proportion of food mass in the diet of palila (Banko *et al.* 2002a). Palila consume flowers and flower buds in the course of searching for pods, but palila densities were not related to flower availability (Hess *et al.* 2001).

This degree of single species dependency on plant foods, primarily seeds, is rare among birds and illustrates unique adaptations that also occurred in other Hawaiian species that are now extinct (Banko and Banko 2009). Palila are morphologically and behaviorally adapted to open unripe māmane pods and consume the seeds, possessing a stout bill for tearing open pods while they grasp them with their feet. Captive-reared palila learned to open māmane pods and consume seeds without the guidance of adult birds, but methods for opening pods and extracting seeds varied somewhat from methods used by wild birds (Frayne 2007), demonstrating an innate ability to recognize and process pods, but also suggesting the benefits of parental teaching (Miller 1998).

There is little information on palila foraging ecology and habitat use from outside of their current range, but historically they likely occurred exclusively in dry forests dominated by māmane. The contemporary diversity of native trees and shrubs in subalpine Mauna Kea is very low (Hess *et al.* 1999), and there are limited opportunities to observe palila foraging on rare plant resources. Although palila were seldom observed using rare alternative foods, they may have eaten fruits of pilo (*Coprosma montana*), ʻiliahi (*Santalanum paniculatum*), ʻākala (*Rubus hawaiensis*), and other dry forest trees and shrubs when they were more common and widely distributed. We observed translocated palila eating portions of ʻiliahi leaves and feeding on the fruits and young green stems of pilo and the fruits of pohā (*Physalis peruviana*) and ʻākala on the northern slope of Mauna Kea. This behavior was not documented on the western slope probably due to extremely low availability (Hess *et al.* 1999). Increasing the availability of a wide range of native plant species appropriate to subalpine Mauna Kea could help palila survive when māmane resources become scarce.

In areas of mixed woodland where browsing ungulates have been culled, māmane regeneration is much greater than naio, and the woodland community is shifting towards māmane dominance (Hess *et al.* 1999). If māmane density continues to increase in the mixed naio-māmane woodland, palila densities may also increase, although they may ultimately be limited by drought (Banko *et al.* 2013). Restoration of māmane in mixed woodland and other areas, such as the northern and southern slopes of Mauna Kea and areas on the western slope adjacent to the core habitat of the palila population, would increase the overall phenological diversity and the likelihood of birds finding more food patches in years of low food availability (van Riper 1980b, Scott *et al.* 1984, Banko *et al.* 2002a). Habitat restoration would benefit the recovery of the palila and allow this highly specialized Hawaiian honeycreeper to recolonize areas within its former range (Scott *et al.* 1984, 1986; Fancy *et al.* 1993, 1997; Banko *et al.* 2009).

Diet

The palila diet consists overwhelmingly of māmane seeds. We found no difference in the diets of adults between the breeding and non-breeding seasons, when nutritional requirements might be expected to shift to high-protein foods, such as insects. We found that caterpillars were an important supplementary food throughout the year in the diets of adult palila, and they were especially important in the diets of nestlings (Banko *et al.* 2002b). *Cydia* caterpillars, which feed within the seeds of māmane pods where they spend their larval life (Oboyski 2011), were the main insect prey in our samples. To be consumed by foraging birds, caterpillars must be extracted from māmane pods, but they may be found incidentally by birds ripping open pods to access seeds. Hatch-year palila require several months of foraging with adults before their strength, coordination, or possibly other factors are sufficiently developed for obtaining māmane seeds on their own (Miller 1998, Banko *et al.* 2002b).

Understanding the diet composition of different age groups may eventually help explain differential survival rates of palila. Nestling palila consumed *Cydia* caterpillars at the highest rate; *Cydia* fragments were found in the feces of virtually all palila nestlings but in less than two-thirds of adult birds. Nestlings are dependent on adults for all of their food, indicating that adult palila feed caterpillars to their chicks more frequently than they consume this food themselves. Of all age classes, second-year palila consumed *Cydia* least frequently, suggesting that experience is needed to forage effectively for caterpillars within māmane pods. Second-year palila consumed other arthropods about as frequently as did other age groups, suggesting that insects found on foliage and branches were exploited equally by self-sufficient birds of all ages but that differences in *Cydia* consumption were due to search efficiency or experience. Auxiliary foods, such as flower stamens, grass seeds, and arthropods other than *Cydia*

(*Scotorythra* spp.), were found more often in feces of nestlings, suggesting that other age groups relied more on māmane seeds.

Although highly specialized on māmane seeds, our results indicated that palila consume other types of food. This raises the possibility that other native plants and arthropods might help sustain palila when māmane seeds are scarce, if they can be identified and made more available to palila. Identifying alternate foods may be challenging, given the relatively low biodiversity of subalpine Mauna Kea following many decades of habitat destruction by feral ungulates (Scowcroft and Giffin 1983) and invasion of many species that disrupt the food web that sustains palila (Banko *et al.* 2002a). Foods that might have been important historically may now be unavailable to palila in their present range. For example, Perkins (1903) found the stomachs of several palila to be full of *Uresiphita polygonalis virescens* (Crambidae) caterpillars, but *U. polygonalis* is relatively uncommon in PCH today, and we found no indication of them in the diets of birds we sampled. New insights about alternate foods could emerge as the habitat recovers from browsing damage, but increasing the abundance and diversity of some native plant species through strategic planting might also reveal important information.

Food Chemistry

We showed that māmane embryos are extremely well-balanced nutritionally and contain relatively low levels of fiber and high levels of carbohydrate, lipid, and protein (a ratio of about 1:2:2), as well as relatively balanced profiles of essential amino acids and minerals (Banko *et al.* 2002c). Based on our estimate of daily seed consumption, the amount of nitrogen and protein consumed by palila is likely to meet their requirements for daily activities. Although we did not assay minor organic constituents, such as vitamins, māmane embryos seem particularly well-balanced nutritionally, which largely explains the heavy reliance of palila on this food for their daily diet and for rearing offspring. We showed that embryos contained high levels of several different alkaloids, including the highly toxic quinolizidine cytisine, which exceeded 1.5% of seed dry mass. Although the physiological mechanism is unknown, the tolerance of palila to such high levels of alkaloid may be the product of intestinal uptake followed by detoxification in the liver (with consequent effects on relative liver size), non-absorption from the gut (unlikely because quinolizidines are lipophilic under alkaline conditions of the gut and should diffuse into the body), or active export via P-glycoprotein-type ATP-binding cassette (ABC) transporters.

Relative to embryos, seed coats contained higher levels of phenolics and fiber, but lower levels of most major nutrients. Palila reject seed coats when they eat embryos, probably because of their lower overall nutritional value and possible negative influence of phenolic-based secondary metabolites. Alkaloid levels in the two hardened seeds that were collected from brown pods were similar to levels in seeds of green pods that were sampled at the same time in early August. This suggests that palila may reject brown pods more on the basis of their toughness than because of seed toxicity, although we did not analyze the nutritional content of the hardened seeds. Additionally, palila may occasionally open brown pods to extract *Cydia* caterpillars that are sometimes found within. Oboyski (2011) found live mature larvae in hollowed-out, dry mature seeds, while in the laboratory some larvae survived for more than 18 months in drying seeds and emerged as adults shortly after the application of a moist tissue, suggesting the capacity for facultative diapause.

In addition to being found conveniently inside māmane pods, our data suggest that *Cydia* caterpillars are relatively non-toxic sources of lipid, protein, and other nutrients, and thus represent occasional, relatively high-quality resources (Banko *et al.* 2002c). In an evolutionary context, relatively non-toxic, nutritious foods would be important to the survival and development of birds that were susceptible to alkaloid toxicity. Although *Cydia* larvae have a much higher level of phenolics than do seed embryos, total phenolics in the insects were similar to the level found in seed coats. Assuming that the phenolics within *Cydia* bodies are of māmane origin and have similar internal, anti-nutritional effects when consumed by palila regardless of the source, seed coats are far less nutritious than are *Cydia* larvae. Our data suggest that *Cydia* caterpillars break down the alkaloids in the course of digestion, and we found no evidence that *Cydia* caterpillars sequester significant quantities of these alkaloids in their bodies.

Both palila and *Cydia* feed heavily within certain trees and lightly upon others, and additional research might identify factors that influence the selection of individual māmane by consumers. A hypothesis to explain this is that seeds of heavily exploited individuals are especially rich in certain required nutrients (lipids, carbohydrates, protein, essential amino acids, etc.); alternatively, favored trees may be particularly low in certain toxic secondary metabolites. An additional unanswered question is what environmental factors contribute to variability in seed chemistry? We were unable to relate the pattern of increasing then decreasing levels of cytisine during summer to environmental conditions, although we did not examine rainfall patterns. Similarly, we did not consider whether rainfall or other factors might account for the relatively minor annual variation in the seed chemistry of individual trees. Our analyses of variation in seed alkaloid levels, though limited, suggest that many trees must be sampled to address the question of whether toxic secondary metabolites can account for preferences by palila or *Cydia*.

To the extent that variability in māmane seed chemistry is genetically influenced, there may be value in including seeds of trees that are favored by palila and *Cydia* in reforestation efforts. Limited observations suggest that trees favored by palila in one year are also favored in subsequent years, but this needs to be tested at a larger spatial and temporal scale. If this holds true, seeds could be collected from favored trees and distributed to ensure that they are widely available to their consumers. Additional analysis may also reveal what fraction of available trees is heavily exploited by palila. This information could help managers better understand the habitat requirements of palila. However caution should be exercised, and the costs to māmane and the dry forest of this level of genetic selection should also be considered.

Food Availability: Māmane Phenology and *Cydia* Caterpillars

In the seven-year (1998–2005) study we describe here, māmane pod abundance peaked relatively briefly and at the same time at all elevations. This contrasts with the results of a 10-year study (1992–2001) in which pod abundance varied seasonally with elevation and was high for many months at any given elevation (Banko *et al.* 2002a). These earlier results indicate that trees distributed along a large elevation gradient can provide māmane pods, flowers, and *Cydia* caterpillars throughout the year (Scott *et al.* 1984, Fancy *et al.* 1993, Lindsey *et al.* 1995, Banko *et al.* 2009), although palila densities are positively correlated with the number of māmane pods at different elevations (Hess *et al.* 2001), and the population is concentrated in areas containing large, mature trees (van Riper *et al.* 1978).

A factor contributing to the greater synchronization of pod production during 1998–2005 was likely the drought conditions that prevailed during most of that time (Banko *et al.* 2013). If true, then a trend toward drier conditions in subalpine Mauna Kea might lead to shorter breeding seasons for the palila, because pods would be abundant across the landscape for less time. Additionally, drought reduces the size of pod crops (Banko *et al.* 2013), and we found that the number of pods per tree in 1998−2005 was half the number recorded in 1992−2001 at high elevation on the western slope.

In our 1998−2005 study, māmane pods were available around Mauna Kea throughout the year, although the actual abundance varied seasonally. Māmane seeds were most available during the palila nesting season, which is generally March through September (van Riper 1980a, Pletschet and Kelly 1990, Banko *et al.* 2002b). The abundance of *Cydia* caterpillars was episodic in all areas of Mauna Kea. The number of *Cydia* per pod peaked in November when pods were relatively uncommon. Presumably as pods become less abundant, *Cydia* become more concentrated in the remaining pods. Nevertheless, the overall availability of caterpillars per tree was highest in June when pods were abundant and many palila were breeding.

The productivity of māmane trees on the western and northern slopes tended to be greater at higher elevations (see also Banko *et al*. 2002a). Investigating factors that reduce flower and pod production at lower elevations could provide useful insights for managing palila habitat at the landscape scale.

Food Availability: Foliar Caterpillars

Caterpillars found on māmane foliage were generally uncommon in the subalpine forests of Mauna Kea. *Scotorythra artemidora* was the most abundant caterpillar collected in both years of the study, but it was collected most frequently in 1999. Possible explanations for these trends are small sample sizes, differences in microhabitats, variation in rainfall, and uneven timing of sampling during the year.

Virtually all caterpillars collected in this study were early instars. This suggests that our daytime sampling was likely biased against older, larger caterpillars, which typically would be expected to spend daylight hours in seclusion while feeding at night (Perkins 1913; M. Heddle, University of California at Berkeley, personal communication). Even so, our sampling took place during the hours when birds would be most actively foraging, which realistically reflects food availability for palila and other birds.

Additional research into the life history of *Scotorythra* and other species of foliar caterpillars would help understand their interactions with host plants and other arthropods. It would be particularly important to determine how forest restoration and the possible increase of other host plant species in PCH would affect the abundance and diversity of moths and caterpillars.

Food Availability: Insect Surveys in the Pu‘u Mali Mitigation Parcel

Although many invasive arthropod threats, including ants, predacious wasps, and parasitoid wasps, were identified in surveys of the Pu‘u Mali mitigation parcel, we did find two moth species formerly thought to be extinct and one undescribed moth species. Additionally, almost all caterpillars we collected were *Uresiphita polygonalis*, which has been observed feeding heavily on māmane and being eaten by palila in the past (Perkins 1903, 1913). Although originally thought to be endemic, Zimmerman and Hardy (1958) concluded that *U. polygonalis* was a naturalized species. Nevertheless, further work is needed to understand its potential as prey for palila at the lower margins of PCH.

Threats to Food Resources: *Cydia* Caterpillar Parasitism

Cydia caterpillars that feed in māmane seeds were parasitized by four widespread generalist wasp species on Mauna Kea: *Pristomerus hawaiiensis*, *Calliephialtes grapholithae*, *Diadegma blackburni*, and *Euderus metallicus* (Brenner *et al.* 2002, Oboyski *et al.* 2004). Historically, *P. hawaiiensis*, *Trathala flavo-orbitalis* [Cameron] (Ichneumonidae), and *Eupelmus pelodes* Perkins (Eupelmidae) were known to parasitize *Cydia* caterpillars in Hawai'i (Perkins 1913, Swezey 1954, Zimmerman 1978), but we did not recover *T. flavo-orbitalis* or *E. pelodes* from *Cydia* caterpillars that we reared. The origins of these species are somewhat obscure, but *P. hawaiiensis* may be endemic.

In both the 1997 and 1998–2001 studies, parasitism rates by different wasp species varied with elevation. Overall parasitism decreased with elevation in 1997, due mostly to the high incidence of two wasp species (*C. grapholithae* and *P. hawaiiensis*) at lower elevations and the inclusion of two low elevation sites in Pōhakuloa Training Area (PTA). In the 1998–2001 study, which excluded the two PTA sites, overall parasitism did not vary significantly with elevation, although parasitism by particular wasp species was related to elevation. A major difference between the two studies was the higher rate of parasitism by *E. metallicus* in 1998–2001, particularly at higher elevations (Oboyski *et al.* 2004). In 1997, *E. metallicus* was distributed more evenly across all elevations. Our results suggested that this suite of parasitic wasps, many of which have been present on Mauna Kea for over 100 years, were partitioning the landscape and its resources to some degree. Nevertheless, parasitism of *Cydia* caterpillars overall was about 40%, representing a major impact on an important food of the palila.

Threats to Food Resources: Foliar Caterpillar Parasitism

Five parasitoid species were reared from caterpillars collected from the foliage of three common host trees and shrubs within PCH. The overall rate of parasitism on the most common caterpillar, *Scotorythra artemidora*, was 26%. *Scotorythra artemidora* was collected from māmane and was attacked by four parasitoid species. *Peridroma albiorbis* that we collected from māmane was also parasitized at a frequency of 26% by three species. The most frequent parasitoid reared from *S. artemidora* and *P. albiorbis* was *Hyposoter exiguae*, an alien wasp that preys on many species of exposed caterpillars. The next most frequent parasitoid we reared was *D. blackburni*, an introduced wasp that also attacked *Cydia* caterpillars within māmane pods (Brenner *et al.* 2002, Oboyski *et al.* 2004). *Chaetogaedia monticola* is a large fly that was purposefully introduced and it parasitized both *S. artemidora* and *P. albiorbis.* Only a few individuals of the intentionally introduced wasp, *Metorus laphygmae*, were reared from *S. artemidora*, but it was the most common wasp reared from *Scotorythra* (new species 15) in PTA training areas 1 and 2 (Oboyski *et al.* 2002).

Parasitism rates reached 47% in *P. albiorbis* at 2,650 m elevation, indicating the potential of parasitoids for limiting the availability of this common caterpillar to foraging birds. Palila may have fed more frequently on foliar caterpillars in the past (Perkins 1913), but we did not find them frequently in palila fecal samples (see Chapter 14: Diet). This suggests that parasitoids may reduce the availability of caterpillars to palila and other native birds.

Threats to Food Resources: Yellowjackets

Although *Vespula* species are especially effective predators of caterpillars, they harvest the most easily obtained arthropods on vegetation or the ground (Gambino and Loope 1992). Consequently, they have the potential to reduce the availability of arthropod prey to palila and other native birds and could start a trophic cascade that might otherwise alter food webs on Mauna Kea.

The abundance of yellowjackets on Mauna Kea varied depending on the slope, year, and elevation. The only consistent pattern was the seasonal cycle of occurrence. The distribution of shrub and herbaceous ground cover, which may affect the availability of preferred prey, might also explain the differences in the abundance of yellowjackets on the four slopes. In particular, abundant pūkiawe (*Leptecophylla tameiameiae*) shrubs may have helped support large yellowjacket populations on the northern and eastern slopes. Yellowjacket nests were significantly more common under pūkiawe shrubs than elsewhere on Haleakalā (Gambino *et al.* 1990). Additionally, over 90% of yellowjacket foraging bouts targeted pūkiawe on Haleakalā, where yellowjackets were attracted to honeydew secreted by an endemic sap-feeding mealybug.

Our results indicate several areas of yellowjacket ecology that warrant additional study on Mauna Kea. The first is to determine the actual impact of yellowjacket predation on native arthropod communities and the ramifications for the entire subalpine ecosystem on Mauna Kea. The second is to confirm that yellowjacket colonies overwinter above 2,200 m elevation on Mauna Kea. The detection of workers during winter months indicates the possibility of overwintering nests nearby, but the implications of overwintering for yellowjacket population dynamics and impacts are unknown. Another research need is to identify yellowjacket nesting habitat and colony distribution on Mauna Kea to improve survey methods and develop control strategies. The palila population is concentrated on the western slope of Mauna Kea (Banko *et al.* 2013), where yellowjacket abundance and occurrence tend to be lowest. Nevertheless, additional studies could determine whether arthropod prey are becoming less available to palila and other native birds due to yellowjacket predation and whether there may be other ecosystem impacts.

Threats to Food Resources: Ants

We collected seven ant species in five surveys over six years, including three species not previously reported in this region. Our results indicated a significant increase in the range of three species, especially *Cardiocondyla kagutsuchi*. Distributional patterns of the three most common species in our survey area differed, suggesting that each species' invasion had a different series of interactions with local habitat conditions or arthropod communities. *Linepithema humile* was distributed in two concentrated populations whose boundaries shifted through time, *Pheidole megacephala* ranged within one relatively fixed area, whereas *C. kagutsuchi* was found scattered over the survey area.

The rapid expansion and patchy distribution of *C. kagutsuchi* suggest that nuptial flights were relatively common on Mauna Kea. Although spreading less rapidly, both *L. humile* and *P. megacephala* were detected at stations far from their main concentrations, suggesting long-distance, jump-dispersal, which might have been aided by human activity. Of particular concern is that *L. humile* suddenly might appear within the nesting range of the endangered palila, potentially putting the birds' eggs, young, and arthropod prey at risk. Further invasion of palila habitat seems likely because this area is traversed by roads and frequented by people. The persistence of *P. megacephala* for six years at 1,900 m elevation, well above its typical range, may indicate adaptation to the local environmental conditions. Relatively little is known about the effects of *C. kagutsuchi* on arthropod communities, although its rapid spread on Mauna Kea, both laterally and in elevation, warrant additional monitoring and research.

Continued invasion of the native woodland and shrubland communities by ants could disturb native arthropod and bird communities through predation, competition, and disruption of food and pollinator webs (Holway *et al.* 2002, Lach 2008). Human activity on Mauna Kea may increase the likelihood of ant invasion through long-distance jump-dispersal. There are no effective tools for controlling ants at the landscape level; therefore, stopping or slowing the spread of ants into PCH may offer the most practical protection for reducing their threats to caterpillars and other arthropod prey of palila. Additional monitoring by baiting and substrate searching to detect ant encroachment into high-elevation palila habitat would help managers to eradicate local invasions before they became widespread and more difficult to control.

Threats to Food Resources: Predacious Ground Beetle

The impact of the introduced, generalist arthropod predator, *Laemostenus complanatus*, on palila food resources is unknown, but like most other carabid beetles, *L. complanatus* preys on other insects. During daylight these beetles were found under rocks, plants, and the loose bark of trees, but at night we observed them moving on the ground or in māmane and naio trees within PCH. Although capture rates of *L. complanatus* dropped markedly between 1992 and 2002, suggesting an overall decrease in abundance of the beetle, its range expanded. Range expansion and the occasional abundance at which we observed it suggest that it could add to the overall impacts of other invasive arthropod predators on food webs and trophic interactions of importance to the palila. Investigating the impacts of *L. complanatus* on palila food availability and the arthropod community of subalpine Mauna Kea could provide useful guidance about the management of this potential food web disruptor.

Vegetation Ecology

Vegetation Structure and Composition

By combining data obtained from satellite imagery with aerial photographs and intensive field surveys, we obtained a detailed thematic vegetation classification for exploring ecological relationships between the palila and its environment. Although we were able to confirm the general boundaries between the major vegetation associations in the Jacobi (1979) aerial photo interpretation, we typically found little correspondence between the remote imagery and tree cover and other attributes measured on our survey plots. Contributing to these differences would have been changes in tree cover since the time of the aerial photographs (due to the limited regeneration of māmane resulting from the annual culling of ungulates) and dissimilarities in the methods used in the two approaches.

Our thematic classification revealed the effects of feral ungulates in PCH and provided a means for predicting changes in forest structure and composition after browsers are completely and permanently removed. We expect that the most dramatic change will occur in the mixed shrub community (type 5). Māmane regeneration was relatively high in this association and the density of māmane is likely to continue to increase if feral sheep (*Ovis aries*), European mouflon sheep (*O. gmelini musimon*), and their hybrids are completely eliminated. Recovery of this habitat would provide a habitat corridor between woodland on the western and northern slopes of Mauna Kea. Currently, palila are restricted to the western slope where they are at risk from a catastrophic event such as a large wildland fire.

Māmane regeneration also was relatively high in bare regions (type 1), where long-term browsing has been especially severe at the tree line (Scowcroft and Giffin 1983). Regeneration near tree line was mostly confined to rocky ridges and was lacking in large expanses of cinder and ash, possibly because rocky cracks create microclimates where young trees can become established. In addition to the recovery of māmane-dominated woodlands, māmane will likely increase in the mixed woodlands at lower elevations due to a higher rate of regeneration following the culling of sheep (Hess *et al.* 1999).

Despite the culling of sheep populations, some areas of heavily browsed habitat are recovering poorly. Tree mortality was high and māmane regeneration was poor in grassy māmane-dominated woodland. In the pasture grasslands (type 9) in PCH that have been leased for cattle grazing, standing dead trees were more common than live ones and regeneration was extremely low.

Our spatially explicit thematic classification of vegetation provides a baseline for longitudinal comparisons to evaluate the effect of management actions such as the eradication of browsers. As sheep are eliminated from PCH, we expect vegetation to be highly dynamic with recovery occurring at different speeds in some regions and vegetation associations. Species dominance will likely change, alien plants may continue to invade, and ecosystem properties may change over time.

Vegetation Survey in Palila Critical Habitat

We identified 180 plant species on the survey of vegetation in PCH. Over two-thirds of the species were alien, including several species that had not been recorded previously on Hawaiʽi Island. Although most herbaceous and grass species were alien, most of the trees, shrubs, and ferns were native.

Although trees were widely distributed in PCH, tree cover was generally patchy and sparse except on the southwestern slope, where naio and māmane were relatively abundant and where palila were concentrated (Banko *et al.* 2013). Māmane was the most broadly distributed tree species, but māmane cover was likely too low to support palila in most areas around Mauna Kea. Nevertheless, a small but relatively dense patch of māmane forest on the northern slope was extensively used by palila translocated there (Banko *et al.* 2009).

Although we recorded māmane trees as tall as 11 m on vegetation plots, most trees in PCH were small, averaging 3.7 m in height. Nearly two-thirds of māmane trees were under 4 m tall, indicating widespread regeneration within the preceding 25 years, based on the growth models of Scowcroft and Conrad (1988). Although māmane saplings (<2 m in height) were found in 91% of survey plots, only 38% of plots contained densities equivalent to at least one sapling per 100 m^2. Thus, the condition of the forest is improving, but not with sufficient speed to prevent steep declines in palila numbers during drought (Banko *et al.* 2013). Forest recovery will proceed more quickly after browsers have been completely removed.

Palila primarily utilize larger māmane trees (Scott *et al.* 1984, Pletschet and Kelly 1990) due to their more abundant food resources, better concealment from predators, and protection from unfavorable environmental conditions. That only 39% of māmane trees were more than 4 m in height indicates that palila spend most of their time in a limited set of trees across the landscape.

We found evidence of sheep and other ungulates on a majority of plots on the southwestern slope, indicating their attraction to māmane as a food source. This evidence also suggests that māmane will increase once browsing is eliminated.

We encountered many dead and dying māmane trees on vegetation plots throughout PCH. We did not identify causes of mortality, but contributing factors may include fungal root rot, browsing, alien weeds, and drought (Banko *et al.* 2013).

The woody vegetation of PCH is dominated by a few native species that are critically important to the endangered palila. This dry, subalpine woodland is dynamic with widespread regeneration of māmane but also with relatively high levels of mortality. Palila recovery can be expedited by increasing māmane cover, which can be accomplished by eliminating browsing ungulates, planting seedlings, sowing seed, and suppressing alien grasses and other invasive weeds that may compete with māmane.

Vegetation Surveys on Mitigation Parcels

Surveys at Puʽu Mali and Kaʽohe established the baseline conditions of the vegetation on the mitigation parcels soon after the termination of cattle grazing. Five individuals of *Bidens campylotheca campylotheca*, a species of concern, were discovered on the Puʽu Mali parcel. The five tree species that were recorded at Puʽu Mali represent the majority of the native tree species expected in this region. This suggests that existing seeds and scattered trees could promote forest regeneration at the local, if not landscape, scale.

Individual trees were concentrated in localized patches within the ʽaʽā flow at Puʽu Mali, whereas Kaʽohe supported fewer tree species, and they were generally more scattered and less abundant. Tree density was lowest on transect 101 at Kaʽohe, suggesting that planting and other management will be needed to accelerate habitat restoration. The disparity in tree distribution between the two mitigation parcels affords an opportunity to attempt different restoration techniques designed for the conditions at each site.

Invasive plants may impede native species recovery in both mitigation parcels. Although both areas have been invaded or are imminently threatened by relatively few habitat-modifying weeds, Kikuyu grass (*Cenchrus clandestinus*) is of particular concern because it forms large, nearly impenetrable mats of vegetation that hinder germination of native shrubs and trees. Other alien species, such as cape ivy (*Delairea odorata*), gorse (*Ulex europaeus*), and banana poka (*Passiflora tarminiana*), which are common on Mauna Kea in places outside of PCH, could also hinder restoration efforts if they are allowed to become established or spread.

Weed Survey in Palila Critical Habitat

In 1999, we surveyed PCH for 15 species of invasive weeds representing the greatest potential for increasing fire hazard, competing with native plants, and facilitating pest arthropods. Nevertheless, the effects of many of these weeds on regional hydrological processes, nutrient cycling, and other ecosystem processes are not well known. The species we selected were somewhat biased towards weeds that were already abundant on the western slope of Mauna Kea, the core of the palila's range (Banko *et al*. 2013). In addition to target species, we noted localized populations of other weeds that posed potential threats and warranted monitoring.

Despite a large source population of fountain grass (*Cenchrus setaceus*) on the lower southern and southwestern slopes of Mauna Kea, the abundance of this serious fire hazard increased only slightly in the 20 years following surveys by Jacobi and Warshauer (1992). Several populations located in 1981 were absent in 1999, but we also discovered a small number of new populations that were not detected 20 years earlier. Nevertheless, the main fountain grass infestation occurred below the area sampled by the 1981, 1999, and 2006–2007 surveys, so we are uncertain about its rate of spread upslope towards PCH. Fountain grass was found mostly in small, disturbed sites, suggesting that native vegetation may replace it once disturbance from ungulates has been eliminated.

Cape ivy also increased modestly since 1980. Although it remained concentrated on the lower western slope of Mauna Kea, it increased in the mixed naio-māmane forest. Satellite populations in the māmane forest at higher elevations were rare in 1999, but indicated its potential for continued spread.

Invading PCH much more rapidly was fireweed (*Senecio madagascariensis*). Fireweed was found at only 10% of our transect stations in 1999, but by 2007 it occupied 86% of stations (*n* = 381) and had spread to tree line around Mauna Kea (U.S. Geological Survey unpublished data).

The threat of fire in PCH is a major concern for palila recovery due to the dramatic spread of fireweed and the longstanding, dense beds of fine fuels formed by invasive grasses, including the six species targeted in our survey (Thaxton and Jacobi 2009). Although widespread on Mauna Kea, orchard grass (*Dactylis glomerata*), velvet grass (*Holcus lanatus*), sweet vernal grass (*Anthoxanthum odoratum*), and Kentucky blue grass (*Poa pratensis*) were rare or absent on the southwestern slope, which is largely dominated by dense naio stands at higher elevations and naio-ʽaʽaliʽi shrubland at lower elevations. Nevertheless, fountain grass occurs extensively on the southwestern slope and has the potential to begin a grass/fire cycle that would be difficult to break. The native bunchgrass, *Eragrostis atropioides*, also is common on the arid southwestern slope and flourished after wildfires in 1991 and 1995 that started along the road skirting the lower edge of the forest (U.S. Geological Survey unpublished data). Further research is needed to determine whether grass/fire cycles based on native grass species may develop on Mauna Kea.

Most of the grasses found on Mauna Kea likely increase the threat of fire, but fire hazard and impact escalate where grass densities are high and the fuel bed is continuous. Grass density was high over several extensive areas of the mountain: 1) mid elevations on the western and eastern slopes where orchard grass, velvet grass, sweet vernal grass, and Kentucky blue grass dominate, 2) lower elevations of the western slope where Natal redtop (*Melinis repens*), perennial ryegrass (*Lolium perenne*), and smutgrass (*Sporobolus africanus*) were common, and 3) low elevations on the southern slope close to Mauna Kea State Park where needlegrass (*Stipa cernua*), purple veldtgrass (*Ehrharta calycina*e), and fountain grass were abundant. Local conditions in each area also may affect fire behavior and impacts. Several alien shrubs, most notably gorse and Russian thistle (*Salsola kali*), also have the potential to change the fire regime, especially if they become more abundant and widespread. Although gorse was concentrated in alien-dominated pasture below PCH on the eastern slope, it has the potential to spread higher and into PCH, increasing the risk of fire.

A wide variety of herbaceous weed species cover PCH. Taken together, herbaceous weeds have considerable potential for displacing native species, although the competitive ability of individual species has not been evaluated. Two vines, cape ivy and banana poka, climb on trees and shrubs, thereby reducing the availability of light, competing for water and nutrients, breaking branches, and suppressing seedlings and saplings (Cuddihy and Stone 1990). Both species of vine spread when ungulates disturb the understory.

Prior to our survey, banana poka had not been reported within PCH. The two plants we found and destroyed on the western slope represented the highest elevation reported for the species in Hawaiʽi and both were heavily laden with fruit that had been partly eaten by birds and rodents. The occurrence of these two individual plants so far away from other known populations and in a highly disturbed site suggests dispersal by humans. Nevertheless, once established and producing fruit, birds or feral pigs could serve as dispersal agents.

Cape ivy was a conspicuous component of mid-elevation mixed māmane-naio forest on western Mauna Kea with smaller satellite populations indicating its potential to spread. Although long distance dispersal is probably common, establishment seems to be rare based upon the few satellite populations we found. Nevertheless, these outlying populations have the potential to expand. We observed that the vines may cover individual trees for over 10 years without killing them; nevertheless, tree vigor and reproduction seemed conspicuously reduced compared to non-infested trees. Cape ivy may also suppress seedlings of native species. Although the vines wilt and die during prolonged drought, the extensive root system allows plants to quickly sprout when rainfall increases.

Weeds also provide food and shelter for many alien invertebrates and some vertebrates, such as the house mouse (*Mus musculus*). Some weeds provide nectar that may help sustain introduced wasps and flies that parasitize the caterpillars of native moths (Brenner *et al*. 2002, Oboyski *et al.* 2004) that are eaten by palila and other native birds. Invasive weeds also may facilitate the spread and sustain populations of other alien insects, such as predatory ants and wasps (Jervis *et al*. 1993, Idris and Grafius 1995), but studies are needed to evaluate interactions between weeds and pests on Mauna Kea. Mullein (*Verbascum thapsus*) was the only targeted herbaceous species we found on the eastern slope of Mauna Kea. Nevertheless, gosmore (*Hypochoeris radicata*) and several clover species (*Trifolium* spp.) were widespread and common and both might provide nectar for invertebrate pests.

Eliminating or controlling weeds in PCH may speed habitat recovery, but more information is needed to demonstrate both the severity of impacts of particular species on the native vegetation and the feasibility of control measures. Many weeds are likely to persist a long time on Mauna Kea, and reducing the consequences of weed invasions may be a more realistic goal than control. For example, since subalpine Mauna Kea is dry with a year-round fire season, fire prevention and suppression and fuel management through the establishment of fuel breaks is needed until tree cover has increased sufficiently to reduce the density of fine fuels (Thaxton and Jacobi 2009).

Eliminating habitat disturbance by feral ungulates is the critical step towards forest recovery in PCH and elsewhere in Hawai'i (Loope and Scowcroft 1985, Banko *et al*. 2009). Efforts to eradicate feral sheep, mouflon sheep, and feral goats (*Capra hircus*) were begun by the Hawai'i Division of Forestry and Wildlife in 1980, and māmane and other native plants are beginning to recover (Hess *et al*. 1999, Banko *et al*. 2009). Feral pigs (*Sus scrofa*) will continue to be managed for sport hunting, although their digging is widespread in PCH (see Chapter 25: Vegetation Survey in Palila Critical Habitat) and it creates favorable conditions for weeds while reducing native plant density (Spatz and Mueller-Dombois 1975).

Although many alien plant species are beyond control, others with small, localized populations might be eliminated through herbicide treatment or hand-pulling. Small populations of banana poka, Russian thistle, California poppy (*Eschscholzia californica*), prickly-pear cactus (*Opuntia ficus-indica*), and coffeeberry (*Rhamnus californica*), all of which have potential for rapid spread and significant impacts on native vegetation, could be eliminated from PCH with prompt attention and regular surveillance for new populations.

It may be possible to stop the spread of some species by eliminating satellite populations. We removed patches of cape ivy by hand at a number of locations above the main infestation on the western slope of Mauna Kea, and these sites were not recolonized even after several years.

Biological agents may also prove useful in controlling some weed species in PCH. Species targeted for biological control are gorse (Markin *et al*. 1996), fireweed (Ramadan *et al*. 2011), and banana poka (Ramadan *et al*. 2008). Lepidoptera are the principal agents being released, and the moth released for fireweed control may also feed on cape ivy in the wild, as it does under quarantine conditions (M. Ramadan, Hawai'i Department of Agriculture, personal communication). Other insects are also being tested against these and other weed species.

To limit the impacts of new weeds in PCH it is important to prevent their establishment. Weeds invade above tree line on Mauna Kea and even the summit area (4,000 m) is vulnerable. In these extreme environments, native plants may be especially sensitive to even low densities of weeds. Precautions and monitoring during the construction of firebreaks, fences, and game bird watering units, would help to reduce the inadvertent introduction of weeds. Although poorly documented, some alien plants, such as coffeeberry and several grass species, were introduced as supplemental food resources for game birds (L. Pratt, U.S. Geological Survey, personal communication). Introducing alien plants in or near PCH could have serious consequences for restoring palila habitat.

A monitoring program would provide information about the rate at which alien species are spreading in PCH and would better identify weeds that might seriously threaten native species and communities. Our survey was designed to provide a quick assessment of the distribution of select weeds and can be easily repeated, as we did in 2007 to document the rapid spread of fireweed. As the subalpine forest recovers from long-term ungulate damage, it will be helpful to anticipate changes in community structure and composition and interactions between native and alien species. Monitoring and research may reveal that some alien plants benefit native communities by preventing soil erosion and providing hospitable microhabitats for native seedlings and invertebrates. On the other hand, control strategies and management capacity are needed for species that clearly threaten PCH. Tree planting and other efforts to restore the forest may be most effective in reducing weed populations and may be necessary to reestablish native species in sites dominated by alien grasses. Grasses and other weeds may be inhibited where tree canopies substantially reduce light availability at ground level and produce sufficient litter accumulation (Thaxton and Jacobi 2009). Forest restoration can be promoted by reducing disturbance by ungulates, fire, and human activity.

Weed Survey on Southwestern Mauna Kea

To evaluate weed threats to PCH from areas immediately below, we surveyed the lower slopes of southwestern Mauna Kea in 1999. We searched for three particularly noxious weed species: fountain grass, cape ivy, and prickly pear cactus.

Fountain grass was recorded at about one-third of all stations, but it was distributed patchily in low densities (often as individuals or small clumps). Most plants were associated with disturbance or gullies that could act as dispersal corridors. Eliminating disturbance from introduced ungulates may reduce the potential for spread to higher elevations, but eliminating small patches in and near PCH would also protect the forest.

Our survey revealed isolated patches of cape ivy outside the main concentration on the western slope. Cape ivy generally spreads by fleshy roots and rhizomes, but viable seeds are produced in Hawaiʽi, and plants flower profusely on Mauna Kea in wetter years, offering an additional mechanism for long-distance dispersal. One patch of cape ivy was growing in a very dry ʽaʽaliʽi shrubland with scattered short trees, suggesting that the potential for invasion in many parts of Mauna Kea is high. Several isolated patches were also identified in pure māmane forest on the western slope in the June 1999 weed survey (see Chapter 27: Weed Survey in Palila Critical Habitat). Furthermore, the problem was not confined to the western slope; a small, but significant clump was noticed on the northern slope in a gully in March 2000 (U.S. Geological Survey unpublished data). Such isolated colonies can be eliminated to prevent further spread. Cape ivy dies back considerably during drought, but individual plants sprout rapidly from rootstock when rains return, suggesting that this weed poses a long-term threat to PCH.

Although we encountered only one prickly pear cactus during our survey, a number of other individuals are known to occur on the southern and western slopes. Three small patches have been identified on Puʽu Ahumoa on the western slope, and two individuals were found upslope of Bradshaw Airfield within PTA on the southern slope. Destroying individuals when discovered will prevent the spread of this species.

Fire Ecology

We investigated the effects of the 1999 Puʽu Loa fire on the subalpine vegetation in wooded pastureland and adjacent ungrazed forest on the eastern slope of Mauna Kea. Ten months after the fire, we inspected all trees within the burn to evaluate mortality and regeneration of ground and epicormic (growing from underneath the bark of a trunk, stem, or branch) sprouts. These data were compared to trees within an adjacent unburned control area 20–100 m outside the edge of the burn. We also assessed vegetation structure and composition within 0.04 ha circular plots (11.3-m radius).

Among the burned areas, alien grass species were less common in forest control plots (U.S. Geological Survey unpublished data), suggesting that fine fuel loading increases following fire. The forested area also harbored species that did not recover from the fire, supporting the idea that fire is rare in this and other native communities in Hawaiʽi (Smith and Tunison 1992). The fire burned with its highest intensity within the forested area, where the density of māmane and fine grass fuels were higher. Grazing by cattle reduced the grass biomass in the pasture, which resulted in a short sward and lower fire intensity. Although two-thirds of the trees in the forest were defoliated, many of these were producing suckers close to their bases. This trend was even more dramatic in the pasture, where a tenfold increase in suckers was observed in the burned area compared to control plots. In addition, the proportion of ground suckers near live trees was twice as high for scorched trees as it was for unburned trees in the pasture, suggesting that low intensity fire can stimulate root suckers. Nevertheless, at high intensities, as was observed in the forest, fire reduced the amount of māmane regeneration. Results from a prescribed burn in Hawaiʽi Volcanoes National Park (HAVO) also suggest a higher rate of root suckering following a less intense burn (R. Loh, HAVO Resources Management, personal communication).

Māmane saplings were more abundant in the burned pasture plots compared to the unburned plots. This may have resulted from decreased competition from the temporary reduction of grass and increased input of nutrients from burned plants rather than the direct effects of heat on seed germination. Māmane regeneration from seeds was not observed following a controlled burn in HAVO (R. Loh personal communication), and māmane seed viability was reportedly decreased by fire (C. W. Smith, Cooperative National Park Resources Studies Unit, University of

Hawai'i at Mānoa, personal communication). Moreover, māmane trees showed little phenological response to fire, suggesting that they did not evolve in a community shaped by frequent fires.

Our results indicate that a low-intensity fire may increase māmane regeneration, but unwanted consequences could be expected. Although carefully implemented controlled burning might promote māmane regeneration within the derelict forest of the pasture, burning could encourage the spread of fire-promoting grasses, which would increase the frequency and intensity of fire. Moreover, other native species (e.g., pūkiawe and *Deschampsia nubigena*) respond poorly to fire (Tunison *et al*. 1993). Therefore, our limited data should not be used to justify controlled burning within PCH to speed māmane regeneration. Instead, planting native species and controlling aggressive alien weeds are more likely to be effective in restoring degraded forest. As tree density increases, grass density may decrease (Thaxton and Jacobi 2009), and a succession of species may follow due to changes in microclimate around the trees. In time, species composition and the increase in moisture due to fog drip may reduce fire potential.

Predator Ecology and Management

Techniques for Determining Predator Activity Patterns

We found feral cats to be very active during daylight hours, but their activity peaked at night between 2000 and 2200 hours, which may have been the most favorable time to forage for rats and roosting birds. The period of lowest cat activity (0400–0600 hours) coincides with the lowest diurnal temperatures at the study site (Juvik *et al.* 1993). Radio signals often became weak or non-receivable during this period, suggesting that cats may have been entering dens or sheltered areas to avoid colder temperatures.

The pronounced diurnal activity pattern that we found in mongooses (*Herpestes auropunctatus*) in subalpine Mauna Kea confirms the findings of other studies (Tomich 1969, Keith *et al*. 1990). A mongoose that we tracked occupied a large home range (at least 1 km^2), which was consistent with home range sizes reported by Tomich (1969) and Keith *et al*. (1990).

We discovered that rats were active from sunset to about 0300 hours. They spent most of their time foraging on naio fruit in the upper canopy of trees. We tried to document rat behavior in the presence of a roosting bird, but no birds were encountered. We located three rat dens in naio trees, two in māmane, and another was underneath a pile of lava rocks. During the life of her transmitter, a female rat occupied a home range of 1,179 m^2. When she was re-tagged seven weeks later, she had moved to a new territory 2,500 m away and occupied a home range of about 650 m^2. A male rat occupied a home range of 2,772 m^2.

Information about the home range size and behavior of feral cats, mongooses, and rats were used in conjunction with the results of other ecological studies to develop strategies for reducing predator impacts in PCH.

Feral Cat Home Range and Movements

Mean home ranges of feral cats on Mauna Kea were the largest reported among seven other studies from the Pacific region for females (772 ha) and the second largest for males (1,418 ha; Goltz *et al.* 2008). We found that home ranges of male feral cats on Mauna Kea were 60% larger, and females were 71% larger than those reported from Hakalau, which is approximately 25 km in distance from our study site (Smucker *et al.* 2000).

We found some evidence that the spatial arrangement and low density of feral cats on Mauna Kea was tied to social organization. There were strong differences between sexes in home range size, which we attributed primarily to mate-seeking behavior in males, and denning behavior in females. Although females on Mauna Kea occupied large areas relative to other study locations, their overall mean home ranges were only 54% as large as males. Nevertheless, their core activity areas were larger than those of males indicating they use smaller areas more intensively while males use larger areas more extensively.

Although we did not find other reports of daily movements in the literature, we documented average daily movements of about 82 m/day and some much greater maximum movements. Because mean daily movements on Mauna Kea did not differ between sexes, males apparently did not always return to the same location on a daily basis, given their larger home ranges, whereas females may have been tied to a central location, such as a den. It is unlikely that all dens were permanent, but some lava tubes were used more than once, sometimes by different cats. Lava tube dens were probably used repeatedly since they provide good shelter.

Male cat home ranges overlapped extensively. There was no overall seasonal pattern to home range overlap, although the range of one male extended to lower elevation primarily during March–August 2001 and then was subsequently centered in higher elevations. Evidence for territorial encounters between males on Mauna Kea comes from the prevalence of feline immunodeficiency virus (FIV), which is primarily transmitted by biting and scratching (Yamamoto *et al.* 1988). While 17% of 39 males from Mauna Kea tested positive for FIV, all 29 females were negative (Danner *et al.* 2007). Overall female home ranges on Mauna Kea overlapped only slightly, and core activity areas did not overlap.

Hansen *et al.* (2007) estimated that 17.6% of cats per generation on Mauna Loa, primarily males, had emigrated more than 53 km from Mauna Kea. Male cats tend to be more wide-ranging than females; therefore, males may encounter more palila and other native birds while foraging. For example, the mean home range of male cats on Mauna Kea represents more than 10% of the entire range (140 km^2) occupied by the palila (Scott *et al.* 1986). Because male home ranges were also nonexclusive, palila may be simultaneously exposed to predation by several different individual cats.

If trapping feral cats is used to protect palila, trap spacing should account for minimum daily movements and differences between sexes in home range. The radius of a circular area equivalent to the home range of female feral cats on Mauna Kea is 1568 m, and for males it is 2125 m. Cats may be expected to encounter traps when traps are spaced at shorter distances, but daily movements may be used to guide minimum spacing between transects during short-term (two-to-three day) trapping sessions. Most subjects moved more than 100 m per day. The implications of large home ranges in male cats are that large trapping areas are needed to confine immigration to buffer zones on the perimeter of endangered species habitat in this environment in Hawai`i.

Other considerations are also important for effective trapping programs. Short *et al.* (2002) found that feral cats that did not use rubbish dumps were more likely to be caught in concealed foot-hold traps than cage traps. Rubbish dumps do not exist within the range of cats on the western slope of Mauna Kea, and other forms of human subsidies are infrequent and small.

Feral Cat and Mongoose Diet

We identified bird remains in 79% of cat and 47% of mongoose samples, indicating a higher incidence of bird predation compared to other studies on Mauna Kea and elsewhere on Hawai'i Island. For example, Hess *et al.* (2007a) found bird remains in less than 30% of cat digestive tracts collected from Mauna Loa and Kīlauea volcanoes in HAVO. Although Snetsinger *et al.* (1994) identified bird fragments in many feral cat scats in subalpine Mauna Kea, rodents were more frequently found. Moreover, our finding of bird fragments in 47% of the mongoose samples was approximately 10 times greater than the frequency reported by Mostello (1996) and Kami (1964). Similar to our results, Kami (1964) reported insects in 41–80% of mongoose scats, but he found a higher incidence of rodent remains (24–72%) compared to our results. Amarasekare (1994) observed rat, mouse, and insect, but no bird fragments in mongoose scats collected on the western slope of Mauna Kea.

Much of the discrepancy in reported occurrences of prey types probably arises from differences in methodology. We expect that examining stomach contents produces more identifiable remains than examining scat, in which contents pass through the entire digestive system. We could often distinguish between gallinaceous and passerine bird fragments in predator stomachs, but we could not distinguish between native and alien passerine fragments. Nevertheless, our findings indicate that the exceptionally high rate of predation on passerine birds by feral cats in PCH poses a significant threat to palila.

Rodent Survey

We conducted 10 rodent surveys for one month biannually during winter (January and February) and summer (June and July) 2000–2005 on the western slope of Mauna Kea to better understand the threats posed to palila and other native birds. We also examined rodent habitat use patterns, morphology, age, sex ratios, and pregnancy rates during selected surveys. We determined rodent arboreal activity in a single, separate, and independent trapping session.

Mice inhabited the māmane, mixed, and naio forests in similar abundances, but rarely utilized pasture, where the grass cover was continuous. The scarcity of mice in the pasture may have been due to increased exposure to predators or to the scarcity of grass seed resulting from Kikuyu grass, a species that spreads vegetatively, dominating the pasture. Cattle grazing may also have kept grass seed availability low. Mouse abundance did not vary significantly in relation to elevation on the western slope. There was a positive, but non-significant, relationship between mouse abundance and six-month median precipitation.

The changes in mouse abundance over all 10 surveys did not seem directly dependent on season (winter or summer), but there might have been a subtle non-seasonal population cycle (Tomich 1986). Mouse and rat capture rates were high throughout the winter 2005 survey, indicating an intense population irruption during that time. The magnitude and length of the irruption were greater than any other recorded since reliable observations were recorded (1970s, P. Tomich, Hawai'i Department of Health [retired], personal communication).

We observed that adult female mice weighed more than adult males, which was inconsistent with other studies in Hawai'i (Tomich 1981). The pregnancy rate was higher in summer (49.1%) than in winter (2.2%).

We found snap trapping to be a more sensitive method of detecting mouse presence than were census blocks, based on the mean probability of mouse detection. Even so, there were fewer than 50 instances (7.3% of station-nights) in which census blocks were more sensitive than snap traps in detecting mice. Our comparison of mouse detection methods did not independently compare census blocks with snap traps, but to do so we suggest: 1) monitoring a transect with one census block per station for four consecutive nights, then 2) monitoring the same transect with one snap trap per station over the following four consecutive nights. This method would yield temporally independent data and provide a more robust comparison of survey methods. Conducting rodent surveys before and after control efforts could help determine the efficacy of diphacinone baits in areas where palila are reintroduced.

The scarcity of rats on the western slope was consistent with results of previous studies and may be attributable to factors associated with high elevation, such as low temperatures or lack of water (Amarasekare 1994) or possibly depredation by carnivores. Although we were unable to determine the relationship of rats to habitat type due to low capture rates, the frequency with which they were trapped near *Santalum* trees suggests some level of attraction. Our finding that both mice and rats exhibit arboreal activity agrees with results from Amarasekare (1993). Mice are not thought to be nest predators or competitors of palila (Amarasekare 1993), but we do not entirely discount their potential to cause disturbance to nesting birds. Video images of a mouse at the nest of a palila were recorded by a surveillance camera (see Chapter 9: Breeding Phenology, Productivity, and Nesting Success), although there was no indication of negative consequences.

Forensic Techniques for Predator Identification

To help identify mammalian predators of palila whose carcasses were found in the wild, we initiated a study to help recognize diagnostic clues left by different species. Our method was to observe predators feeding on the carcass of a small bird in a controlled setting to determine whether the predator could be identified solely on clues observed on the carcass. We observed predator feeding habits, videotaped their behavior, and described and cataloged the remains. We used this information to develop methods and skills for identifying species responsible for nest destruction and bird mortality.

Using our methods, the remains of dead palila sometimes provided clues to the identity of the predator that killed them. Nevertheless, scavengers usually could not be distinguished from predators. Scat, hair, and tracks provided important evidence in determining predator and scavenger identity.

Impact of Predators at Bird Nests

We monitored wild bird nests on two 500 x 500 m grids in māmane forest and mixed māmane-naio forest on the western slope of Mauna Kea in 1999 to determine the impact of introduced mammalian predators. Predation at nests on both study grids occurred at similarly high levels (56.2% in māmane and 57.1% in mixed forest). However, fledgling production was higher on the māmane grid, where 43.8% of nests fledged at least one chick, than on the mixed forest grid, where 21.4% of nests fledged a chick. Three nests in the mixed forest grid were abandoned possibly due to prolonged rain and cold weather in late February 1999.

Our failure to capture rats in 2,360 trap-nights on the two study grids supports other findings of low rat density on the western slope. The lack of trapping success could reflect seasonal or annual variation in rat population levels or a decline in rat densities due to drought conditions that prevailed during the study.

Mouse abundance was also lower in our study than has been reported previously (Amarasekare 1994, see Chapter 33: Rodent Survey). Low abundance supports the idea that drought may have depressed rodent populations during the 1999 breeding season. Mice are not known to be predators or competitors of palila (Amarasekare 1994), but mice climb trees and may disturb palila at their nests, especially during the egg stage. In addition, owls prey on native birds on Mauna Kea (Snetsinger *et al*. 1994, Klavitter 2009). Detecting the impact of these predators, however, is much more problematic than for mammals because they may leave no trace at nests. In such cases, it may be difficult or impossible to confirm depredation of specific nests by owls without the use of surveillance cameras. The two types of tracking boards we placed at nests were not effective in detecting predators of any kind.

Predator Management

We tested techniques for removing predators on the northern and western slopes of Mauna Kea during 1998–2005. Methods for reducing feral cat and mongoose numbers focused on the effectiveness of different spatial and temporal distributions of live traps during nine sessions. Research into reducing rat threats consisted of varying the placement and duration of poison baits. The ultimate response variable of interest for both rats and carnivores was the effect of different treatments on the depredation of palila. Nevertheless, due to personnel limitations, we used predator abundance as a proxy for depredation rate.

Overall capture rates for feral cats during our study were similar to capture rates recorded during other studies on Mauna Kea, although our capture rates ranged between 0.64–7.42 per session. The wide range in capture rates may partly reflect environmental variability in subalpine Mauna Kea over six to eight years of trapping effort. Additionally, changes in the cat population through removal (by trapping), reproduction, and environmental factors such as prey availability, may have affected capture rates among sessions.

Controlling the feral cat population on Mauna Kea may not require continual, high-intensity trapping as we found that many cats were removed during the initial 1,000 trap-nights. Feral cat capture rates declined significantly during sessions 3 and 8 and non-significantly during sessions 6 and 7. After decreasing, the capture rates during the longer trapping sessions stabilized at a lower level, suggesting continued low-level immigration from surrounding areas after the removal of all resident cats. Nevertheless, cat capture rates increased significantly in session 9. The beginning of session 9 trapping coincided with a rodent irruption on Mauna Kea (see Chapter 33: Rodent Survey), and the overabundance of prey may have made our baits less attractive. Moreover, the abundance of food may have increased cat survival, reproduction, and immigration, potentially increasing the number of cats available to be trapped later in the session. Because cat trapping may be an ineffective control method during rodent irruptions, the availability of natural prey should be considered before beginning a trapping program.

Interruptions between and during our trapping sessions suggest that breaks of up to two months did not affect the subsequent cat capture rate. On the other hand, long breaks in trapping were followed by higher capture rates, as we observed on the western slope during the initial 150 trap-nights of session 7, which began 10 months after the conclusion of session 6. The high cat capture rate and high percentage of juveniles captured during session 7 (July and August) may have been due to juvenile dispersal from the surrounding areas. Alternatively, low prey availability may have accounted for the increased capture rate as animals may have expanded their home ranges in search of food. Session 7 occurred during a dry year when rodent populations were relatively low (Chapter 33: Rodent Survey), possibly increasing the attractiveness of our baits.

Our estimated initial abundance of cats was always lower than the actual number of cats removed during that session. This may have been an artifact of our circulating trapping effort. Approximately 600 trap-nights were required to cover the entire trapping area. Therefore, we would not expect to capture all resident cats until we had trapped throughout the entire area. Immigration could also have affected capture rates, as may have occurred in session 6.

Although our overall mongoose capture rate was lower than that of van Riper (1978), his result was bracketed by the range of our capture rates per session (0.38–3.94). We found that mongooses bred primarily in the summer months but also bred during the winter. Therefore, we expected the majority of juvenile dispersal to occur in the late summer or fall. Nevertheless, trapping data from session 6 suggested that juveniles were more abundant during May–July. Mongoose capture rates decreased significantly during the only long session without diphacinone application (session 6). Even so, we still captured animals regularly up to about 2,000 trap-nights during session 6. Current carnivore trap arrays are spaced according to cat movement data, and our results suggest that closer trap spacing may be more effective for mongoose control. In addition, very young mongooses were able to escape from our live traps. The lack of mongoose captures where diphacinone bait was applied to control rodents suggested that poison bait was effective for mongoose management. Intensive poison baiting on a larger grid before reintroducing palila to an area, during the nesting season, and during mongoose dispersal may be the most effective methods for protecting palila from mongooses (Hays 1999).

Rats and mice entered diphacinone bait boxes and consumed bait. Mice depleted diphacinone baits quickly, making it necessary to continually stock bait stations with diphacinone to remove rats. Although we did not evaluate changes in rodent populations before and after distributing diphacinone, we observed dead mice at the bait stations. Although poison-killed rodents might pose a potential hazard for `io (*Buteo solitarius*) and other raptors, results of other studies suggest that rats tend to die underground or in other inaccessible locations, thus minimizing threats (Lindsey and Mosher 1994, Spurr *et al*. 2003). Secondary poisoning is even less likely to occur due to the low number of poisoned rodents we found outside bait stations and the small number of `io we saw or that were reported (Scott *et al*. 1986, Klavitter 2000) in subalpine Mauna Kea.

Palila experience less predation when measures are taken to reduce populations of small introduced mammals. During the 1999–2001 palila nesting seasons, when there was no predator control on the western slope, feral cats depredated 8–11% of active nests annually (see Chapter 9: Breeding Phenology, Productivity, and Nesting Success). In contrast, we observed no nest predation by cats during the 2002 breeding season, when we trapped intensively. Additionally, we did not control small mammal numbers during the second translocation trial, and we implicated rats in the deaths of two palila and the deaths or scavenging of three others (see Chapter 2: Translocating Wild Palila). Predation decreased markedly during the third, fourth, and fifth translocation trials.

This study demonstrated that removing small introduced mammals can be effective in reducing predatory threats to the palila and other native birds on Mauna Kea. Our trapping program also led to practical information about the population genetics, demography, diseases, and habitat relationships of feral cat populations in Hawai`i (Hess *et al*. 2007b,c). The genetic structure of feral cats in Hawai`i indicates great dispersal ability between the slopes of Mauna Kea and even between the volcanoes of Hawai`i Island (Hansen *et al.* 2007). This suggests that control will be difficult due to high rates of immigration as cats are removed from areas. Moreover, high rates of reproduction and survival can be supported by abundant bird prey, and male cats may be limited more by the availability of mates than of food (Hess *et al.* 2007b). Relatively high survival (to 11 years of age) and reproduction also allows individual cats to affect palila for many years and enables cat populations to recover quickly after control efforts (Danner *et al.* 2010). Feline immunodeficiency virus, feline leukemia virus, and *Toxoplasma gondii* may depress the feral cat population on Mauna Kea to some degree, but their occurrence suggests they would not be effective agents in a biological control strategy (Danner *et al.* 2010). Cats were captured more often on the western slope and in māmane woodland (Hess *et al.* 2007c), and increasing control efforts near sites of multiple captures may prove more effective than trapping uniformly across the landscape. The number of mongooses captured at a trap was positively correlated to the number of cat captures even though mongooses pre-empted traps; therefore, using alternate control measures, such as diphacinone, might increase the rate of cat captures (Hess *et al.* 2007c). Our extensive research on feral cats and other introduced small mammals on Mauna Kea provides additional information that can be used in an adaptive management framework to improve the effectiveness of predator control to protect palila (Hess *et al.* 2007c, 2009).

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