Chiricahua Mountains Research Symposium

PROCEEDINGS

Editors
Andrew M. Barton and Sarah A. Sloane

Pine Canyon United Methodist Camp
Chiricahua Mountains, Cochise County, Arizona

16-17 March 1992

Sponsored by:
National Park Service,
USDA Forest Service,
Southwestern Research Station of the
American Museum of Natural History,
and the Nature Conservancy

Organizers

Richard L. Anderson, Chiricahua National Monument, United States Park Service, Dos Cabezas Route Box 6500, Willcox, AZ 85643
Andrew M. Barton, Department of Biology, University of Michigan, Ann Arbor, MI 48109
J. Carrie Brown, Douglas District, Coronado National Forest, USDA Forest Service, RR#1, P.O. Box 228R, Douglas, AZ 85607
Sarah A. Sloane, Museum of Zoology, University of Michigan, Ann Arbor, MI 48109
Wade Sherbrooke, Southwestern Research Station, Portal, AZ 85632
Jeanne Wade, Douglas District, Coronado National Forest, USDA Forest Service, RR#1, P.O. Box 228R, Douglas, AZ 85607

Published by:
Southwest Parks and Monuments Association
221 North Court
Tucson, AZ 85701

December 1992

PREFACE

The Proceedings presented here are from the Chiricahua Mountains Research Symposium held from 16-17 March 1992 at the Pine Canyon United Methodist Camp in the Chiricahua Mountains. The primary purpose of the symposium was to provide a multidisciplinary forum for information exchange and discussion regarding natural science (biology, geology, environmental studies) research in the Chiricahua Mountains. Oral presentations were invited from all scientists carrying out such research or its application to management in the Chiricahua Mountains and surrounding basins. Several presentations, including the evening address by Jerram Brown, were solicited by the symposium organizers. The papers included in this volume are based on presentations given at the symposium and are primarily summaries of research to date. Development and peer-review of proceedings papers were entirely the responsibility of the authors.

In addition to these talks, the symposium included a welcome by Jeanne Wade (District Ranger of the Coronado National Forest Douglas District, which includes the Chiricahua Mountains), an opening address by Thomas Hoekstra (Assistant Director of the Rocky Mountain Forest and Range Experiment Station), a special presentation on Cave Ecology by Jerry Trout (Cave Specialist for Coronado National Forest), and a panel discussion of organizational perspectives on research by representatives of most of the public and private agencies managing land in and around the Chiricahuas. During the evenings, attendees participated in round-table discussions on several topics, including planning for an international Sierra Madre-Sky Island conference, recreational planning in the Chiricahua and surrounding mountains, and mechanisms for promoting research in the Chiricahuas.

We gratefully acknowledge the tremendous amount of work of the other organizers: J. Carrie Brown, Wade Sherbrooke, Jeanne Wade, and especially Richard Anderson, who was largely responsible for the concept and successful execution of the symposium. The symposium and these proceedings could not have gone forward without the help and resources of Chiricahua National Monument, Coronado National Forest (Douglas District), the Nature Conservancy, and Southwest Parks and Monuments Association. Finally, we greatly appreciate the hospitality and efficiency of Gary Harmon and staff of the Pine Canyon United Methodist Camp.

Andrew M. Barton
Sarah A. Sloane

The University of Michigan
Ann Arbor, Michigan

TABLE OF CONTENTS

KEYNOTE PAPER

THE PHYSICAL ENVIRONMENT OF THE CHIRICAHUA MOUNTAINS

THE ECOLOGY OF FORESTS AND PLANTS IN THE CHIRICAHUA MOUNTAINS

THE ECOLOGY OF ANIMALS IN THE CHIRICAHUA MOUNTAINS

OTHER ECOLOGICAL APPLICATIONS IN THE CHIRICAHUA MOUNTAINS

SOME MODELING APPROACHES TO THE ECOLOGY OF MOUNTAIN ISLANDS

A Long Term Study of the Mexican Jay in the Chiricahua Mountains

Jerram L. Brown and Esther R. Brown
Dept Biological Sciences
State University of New York
Albany, NY 12222

Cave Creek Canyon in the Chiricahua Mountains has special importance in the study of social birds, particularly for those species in which parents are aided in the rearing of their young by additional individuals, called helpers. Rearing systems with helpers are found most frequently among non-migratory species whose foraging behavior and diet allow them to survive the relatively harsh nonbreeding seasons on their breeding territory. Species with these characteristics tend to be more frequent in southern parts of North America, where winters are less severe. For those of us who do not live in the South, it can be difficult to find a suitable study area to study species with helpers. In the Chiricahua Mountains these species include the Mexican Jay (Aphelocoma ultramarina), the Acorn Woodpecker (Melanerpes formicivora), the Bushtit (Psaltriparus minimus), and perhaps others. In 1969, when we needed to find an area in which to study helping behavior in the Mexican Jay (known from 1983-92 as Gray-breasted Jay), the search was limited because of the southerly range of this species to Arizona, New Mexico,and Texas. We had studied these jays previously in Madera Canyon, Arizona in 1958; but conditions there were unsuitable for longer study because of the presence of too many people. Fortunately the Southwestern Research Station at Portal, Arizona and the Coronado National Forest provided the necessary combination of natural habitat, isolation, encouragement and accommodations.

The ability to recognize individuals can be a powerful tool for studying the behavior and ecology of wild animals. To do this in our study we applied colored plastic bands to the legs of over 1,400 nestling and full-grown jays. Each jay could then be recognized as an individual by its unique combination of color bands. With the Mexican Jay the ability to recognize individuals proved to be especially useful. Every year we have attempted to locate every individual in the population, record its movements between flocks and determine its reproductive success. Because these jays typically live their entire lives in a very small area, usually one or two adjacent territories, it has been possible to follow hundreds of individuals throughout their lives. Since their lives are often long, we have been able to follow some individuals for many years. The results fall into two categories, one relating to individuals and the other to the population. We present here a brief overview of our results. For references and further details see Brown (1987, 1990).

The Individual and Its Group

Our first discovery using color-banded Mexican Jays was that the small groups of 5 to 15 in which they live were nearly constant in size and composition, unlike groups of the Steller's (Cyanocitta stelleri) and Scrub (Aphelocoma coerulescens) jays in the West, which are transient and shift greatly in composition. Every day the same individual Mexican jays were found together on the same areas. After observing fights and chases where groups came in contact we concluded that each group defended its own territory against neighbor groups This is, therefore, a social organization based on group-territoriality, not on the much more frequent pattern of pair-territoriality.

The group is, consequently, a major influence in the life of each individual. A group changes in composition through death of its members, hatching of young, and rare dispersal movements between groups. Although there is a gradual turnover in the membership of a group, it remains an entity; and the group-territorial boundaries tend to remain stable year after year. For example, of the six groups that we began to study in 1969 and 1970, five were still on their same territories in 1992, and the sixth had moved only a short distance. Thus the groups are basically "immortal"; they outlast the lives of their members and possibly their human observers.

Within each group is a dominance hierarchy, as one might expect; but the hierarchies of Mexican Jays are not structured according to conventional wisdom with young at the bottom and strict dominance of males over females. To our surprise we found that jays in their first winter are sometimes at the top of the hierarchy. Although they are probably more desperate for food because of their inexperience in foraging, they must nevertheless fight to obtain dominance, as we have observed many times. Also surprising was the large overlap of the sexes in rank. Although usually ranking lower than males, some females ranked above some males, especially when young. In some flock-years the dominant bird was a yearling female.

Another feature of the Mexican Jay social system that is unusual in group-territorial birds is the breeding within the same territory of three or four females together with a variable number of males, instead of the usual single breeding pair per territory. These multiple female units do not subdivide the territory into subterritories; all pairs share the same territory and every individual can go anywhere within the group territory. Consequently, there is much greater opportunity for both interference and cooperation in various aspects of breeding and rearing young.

The first manifestation of interference when the breeding season begins is the competition for mates and nests. The sight of four or more birds at a nest at this season signifies conflict and tension, not cooperation. A dominant male may become interested in the female of a subordinate male. Or a dominant female may avoid the labor of nest building by taking over the nest of a subordinate female. More commonly, when jays are building the nest lining, which is composed of rather scarce fine fibers, such as animal hairs and plant fibers, they may simply rob these materials from another nest that already has them. Mexican Jays frequently rush to their nests and sit on them for no apparent reason with others in pursuit. We interpret this behavior as an attempt by owners to protect the lining of their nest from robbery and destruction.

Cooperation or altruism is well known in the Mexican Jay. It was among the first species in the world in which sharing of the feeding of the nestlings by the parents with helpers was studied quantitatively using color-banded birds. Most flock members in this species share in the feeding of nestlings regardless of whether they are themselves parents or not. Of course, the sharing isn't equal; parents do more than an even share and young birds in their first nesting season do less on average. Nevertheless, for the parents to be relieved of about half of the burden of rearing young by the helpers is a significant lightening of their load.

The Population

The fact that we can recognize each individual in our population of six to nine flocks means that we can obtain information about their population that is much more accurate than it would be without color-banding because we know the age of most individuals precisely and can trace their movements and reproductive histories. These advantages are especially revealing in long-lived species.

Mexican Jays live a long time for a bird of their relatively small size (130g). About five per cent of the population is at least ten years old, and two individuals have reached the age of 19 years. Thus some of our jays are older than some of the adult people who observe them. Once they reach age one, the annual rate of survival for all ages is about 0.82.

With a relatively long life expectancy compared to other birds, Mexican Jays can afford to delay reproduction a few years until they are more competent at foraging and dealing with their complex social environment. Only once has a bird bred as early as age one, and most individuals are not recorded with a nest until the age of three or four. Some delay even longer, one to 14 years of age. After they begin, they tend to breed every year until their disappearance.

Reproductive success in this population varies greatly from year to year. Furthermore, winters with high survival of the young of the year are unusual. Years in which high production of young are followed by high survival are rare. The result is that jays hatched in certain favorable years are disproportionately common in the population; jays hatched in "bad" years are rare as adults.

Annual variation in reproductive success in the Chiricahua Mountains is keyed to precipitation. Reproduction is poor in dry springs and is enhanced by precipitation in the preceding monsoon and winter. Jays feed a variety of invertebrates to their nestlings. Without sufficient moisture these foods are scarce. In periods of drought fewer females lay eggs and more nestlings starve.

Annual survival of adults, on the other hand, does not vary greatly among years. After a severe failure of the acorn crop in 1989, however, survival of young of the year over the winter was near zero and dispersal movements by the few surviving young were extreme.

In most species of birds the young leave home for good in the first few months or their first year. In contrast, most individual Mexican Jays never leave home. Their entire lives are lived in the territory where they were hatched. For those that are known to survive to breeding age, however, only about half of the members of each sex remain at home; most of the others move only once in their lifetime, and this is merely to a contiguous territory for the vast majority.

Consequently, Mexican Jays often have close relatives in the same flock and sometimes in neighboring flocks. Helpers are commonly related to the young they feed although a close relatedness can often not be demonstrated. Despite the presence of close relatives when choosing a mate, inbreeding is largely avoided. In only about 5% of breeding pairs is the male known to be related to the female. One reason for this rather low amount of inbreeding (compared to what might be expected in this system) is the dispersal pattern of siblings. In general, sisters tend to leave flocks that contain brothers hatched in the same nest but are much less likely to move away from nestmate sisters.

Conclusions

In 25 years of research on the Mexican Jay we have uncovered many aspects of their behavior and ecology that could only have been discovered in a long term study of individually marked birds. Mexican Jays have proven to be surprising in their extreme longevity, delay of reproduction, lack of or reduced dispersal, complex mating system and general sociality. Through

contirued observation of the same individuals over many years we have also come to know their personalities, their idiosyncrasies and individual histories of maturation, breeding and demise. Compared to other North American birds the social system of the Mexican Jay is unusually complex and the demographic extremes mentioned above are unmatched.

Acknowledgements

We thank the Southwestern Research Station of the American Museum of Natural History, the United States Forest Service, and private landowners for access to their land and use of facilities. Financial support was provided by various grants from the United States Public Health Service, the National Science Foundation and by our own funds.

Literature Cited

Brown, J. L. 1987. Helping and Communal Breeding in Birds: Ecology and Evolution. Princeton,NJ: Princeton University Press.

Brown, J. L. & Brown, E. R. 1990. Mexican Jays: uncooperative breeding. In Cooperative breeding in birds: long-term studies of ecology and behavior. (Eds. P. B. Stacey & W. D. Koenig), pp. 268-288. Cambridge:Cambridge University Press.

THE PHYSICAL ENVIRONMENT OF THE CHIRICAHUA MOUNTAINS

ROADSIDE GEOLOGY OF THE CENTRAL CHIRICAHUA MOUNTAINS--
A GEOLOGIC SYNOPSIS OF THE TURKEY CREEK CALDERA

Edward A. du Bray and John S. Pallister
U.S. Geological Survey-MS 905; BOX 25046, DFC; Denver, Colorado 80225

Introduction

In the Chiricahua Mountains faulting and erosion have exposed a three dimensional view of the volcanic and shallow plutonic levels of a large explosive volcano known as the Turkey Creek caldera (Fig. 1). The largest eruption produced 500-1000 km^3 of incandescent ash and pumice, which accumulated while still hot and welded back together to form the 400-m thick Rhyolite Canyon Tuff. Lava flows and volcanic ash and pumice erupted from the caldera record the compositional evolution of the underlying magma reservoir. The caldera's shallow levels have been exhumed, exposing the roof of the long-ago cooled and crystallized magma reservoir. Isotopic data indicate that the caldera developed about 26.9 million years ago (Ma) during a relatively short-lived series of volcanic eruptions. The Turkey Creek caldera is the result of the waning stages of subduction of the Pacific plate beneath western North America, a process that ended by development of the paleo-San Andreas fault system and the beginning of regional tectonic extension in the Basin and Range province of the western United States (Atwater, 1970).

Geology of the Turkey Creek Caldera

We have completed 1:24,000-scale geologic maps of three 7.5' quadrangles (Pallister and others, in press; Pallister and du Bray, in press; and du Bray and Pallister, in press); several other quadrangles are the subject of ongoing fieldwork. Our work (du Bray and Pallister, 1991) shows that the Turkey Creek caldera is a 20-km-diameter volcanic collapse structure that developed as a result of eruption of the Rhyolite Canyon Tuff. The caldera occurs in a terrane of Precambrian crystalline rocks overlain by a thick, faulted and folded sequence of Paleozoic sedimentary rocks, by Lower Cretaceous Bisbee Group sedimentary rocks, and by Tertiary, pre-caldera volcanic rocks (Fig. 1).

Caldera evolution involved three principal igneous events:
1) the near-instantaneous eruption of a voluminous rhyolite ash-flow tuff and concomitant caldera collapse caused by magma withdrawal from a large, shallow magma reservoir
2) emplacement of a dacite intrusion within the collapsed floor of the caldera, which caused the caldera's core region to be bowed up, forming a shallow marginal depression (moat) within the collapse crater; simultaneously dacite lava flows were erupted into the developing moat
3) renewed magmatism, which caused the caldera to be filled with lava flows and minor associated tuff of the moat rhyolite sequence.

Caldera collapse accompanied eruption of 500 to 1000 km^3 of high-silica rhyolite ash and pumice that was deposited both outside the caldera (outflow facies Rhyolite Canyon Tuff) and ponded to great thickness (>1.2 km) inside the caldera (intracaldera facies Rhyolite Canyon Tuff). One of the largest erosional remnants of outflow tuff is exposed north of the caldera in Chiricahua National Monument (Fig. 1). The outflow sequence (approximately 400 m thick in the Monument) consists of multiple ash flow deposits that resulted from a series of incandescent ash- and pumice-charged density currents that spread laterally from the caldera and accumulated in topographically low areas during the paroxysmal eruptions. Latta (1983) recognized that the intracaldera facies is akin to only the uppermost part of the outflow facies. The intracaldera tuff is locally rich in rock fragments, and several wallrock landslide blocks are locally enclosed in tuff. Zones of coarse breccia with house-size blocks are common near the base of intracaldera tuff accumulations but are rare at the current level of exposure in the Turkey Creek caldera; in addition the caldera floor is not exposed.

Subsequent to the caldera-forming eruption and deposition of Rhyolite Canyon Tuff, dacite intruded the intracaldera tuff as a shallow tabular body and was erupted as lava flows. Intracaldera Rhyolite Canyon Tuff above the intrusion (for example, near the head of Turkey Creek) is tilted radially away from the center of the caldera, suggesting that emplacement of the dacite caused the overlying tuff to be domed. The dacite lava flows, well exposed in cliffs south of the Onion Saddle Road in the headwaters of Pinery Creek (Fig. 1) and near Centella Point (Pallister and others, in press), were erupted from an inferred ring dike that intruded the caldera ring fault system and forms the outer, upturned margin of the intracaldera intrusion. Thick dacite lava flows accumulated to a thickness of >0.5 km. The inference that some dacite was erupted as lava flows is indicated by the fact that these rocks are locally glassy and/or vesicular and form horizontal, flow-ramped surfaces capping columnar-jointed zones and glassy flow-breccia horizons.

A period of volcanic quiescence and erosion is indicated by a sequence of sedimentary rocks that overlie intracaldera tuff and are overlain by moat rhyolite. These deposits are mainly poorly-sorted and crudely-bedded breccias and ash-rich sandstone that were deposited on or near the caldera wall and within the caldera moat. A thick (-100 m) section of breccia and sandstone fills a paleovalley cut through the Rhyolite Canyon Tuff and into dacite. This relation demonstrates an erosional interval of sufficient duration for cooling of the dacite and deep erosion prior to eruption of moat rhyolite.

Eruption of high-silica rhyolite magma as a voluminous sequence of rhyolite lava and associated tuff was the final magmatic event in the development of the Turkey Creek caldera. The pre-erosion volume of moat rhyolite is estimated to be —135 km^3. The basal lava in the caldera moat sequence is a small-volume, crystal rich, low-silica rhyolite. The basal moat rhyolite is overlain by three mappable units of crystal-poor high-silica rhyolite lava and minor tuff. Despite complex internal flow folding, such as that seen in outcrops along the road to Methodist Camp (Pallister and others, in press), individual lava-flow map units are remarkably planiform sheets, with maximum thicknesses of 150-300 m and areal extents that exceed 100 km^2 (du Bray and Pallister, 1991). Rhyolite dikes and feeder zones for the moat rhyolite are rare; the moat rhyolite units may overlie their own vents.

Isotopic data are consistent with all of the Turkey Creek caldera rocks being broadly cogenetic. Incremental heating $^{40}Ar/^{39}Ar$ ages on sanidine (LW. Snee, U.S. Geological Survey, unpub. data, 1989) for the Rhyolite Canyon Tuff and the dacite are 26.9+0.1 Ma, whereas ages for two samples of moat rhyolite are 26.9±0.1 and 26.6±0.1 Ma. These ages constrain the erosional interval between emplacement of dacite and moat rhyolite to $<300,000$ y.

Evolution of the caldera

Mid-Tertiary magmatism in the Chiricahua Mountains began at about 32 to 28 Ma, with the eruption of basalt, exposed near Onion Saddle (Pallister and others, in press), emplacement of small granite plutons, and eruption of the voluminous dacite and rhyolite lavas and pyroclastic flows, spectacularly exposed near the mouth of Cave Creek (Fig. 1), that predate the Turkey Creek caldera. Caldera evolution can be described in five stages:

Stage 1: Developement of a compositionally stratified magma chamber at a shallow level in the crust. Rhyolite overlay dacite above a sharp interface (10 percent SiO_2 gap) in the magma chamber.

Stages 2 and 3: Eruption of Rhyolite Canyon Tuff. The lower members of the tuff were either not deposited within the caldera because it had not yet collapsed sufficiently, or they were deposited, but are currently hidden beneath an intracaldera dacite intrusion (stage 4). During the waning phase of stage 3, the compositional interface between high-silica rhyolite entered the ring vent eruption conduits. Mixing of the two magmas was limited, but mingled magmas were locally erupted along what is now the crest of the Chiricahua Mountains (Flys Park) (Pallister and others, in press).

Stage 4: Continued rise and eruption of dacite from ring vents, accumulation of thick dacite lavas in the developing caldera moat, and intrusion of the dacite within the intracaldera tuff. Stratigraphic relations, the mingled rocks, and overlapping ages indicate that both Rhyolite Canyon Tuff magma and dacite magma were present in the source reservoir. Dacite magma from beneath the interface was drawn up into and erupted from vents that previously fed ash-flow eruptions; geophysical evidence suggests that some dacite was trapped in and beneath the vents and solidified to form a ring dike at depth. We believe that the intracaldera intrusion is a thick (>1 km) flat body (a laccolith), rather than the roof of a vast subterranean pluton (Marjaniemi, 1969; Lipman, 1984). Interpretation of the intrusion as an intracaldera laccolith readily explains a lack of both floor rocks and coarse breccias within the caldera and the absence of intracaldera equivalents of most of the outflow tuff. Doming of overlying tuff accompanied intrusion of the laccolith.

Stage 5: Erosion and sedimentation followed by moat rhyolite eruption. Erosion cut through the intracaldera tuff and into the cooled dacite. Sedimentary rocks, rich in Rhyolite Canyon Tuff debris, were deposited in the caldera moat and on the wall of the eroded back caldera wall. Following the erosional interval, rhyolite was again erupted, filling the caldera moat with —135 km^3 of mainly crystal-poor high-silica rhyolite. Eruption of moat rhyolites records generation of a voluminous new batch of mainly high-silica rhyolite with a distinct geochemical signature.

Initially, our continuing studies in the Chiricahua Mountains will involve additional geologic mapping; we hope to complete our understanding of the distribution of volcanic rocks related to the Turkey Creek caldera. In addition, we plan to conduct various topical studies that will help us refine concepts regarding the mechanics of caldera formation and of compositional zonation within the caldera's igneous components.

Literature Cited

Atwater, T. 1970. Implications of plate tectonics for the Cenozoic tectonic evolution of western North America. *Geological Society of America Bulletin* 81: 3513-3536.

du Bray, E.A., and J.S. Pallister 1991. An ash-flow caldera in cross section--ongoing field and geochemical studies of the mid-Tertiary Turkey Creek caldera, Chiricahua Mountains, SE Arizona. *Journal of Geophysical Research* 96: 13435-13457.

du Bray, E.A., and J.S. Pallister in press. Geologic map of the Chiricahua Peak quadrangle, southeast Arizona. *U.S. Geological Survey Geologic Quadrangle Map.* scale 1:24,000.

Latta, J.S. 1983. *Geochemistry and petrology of the ash flows of Chiricahua National Monument, Arizona, and their relation to the Turkey Creek caldera:* MS thesis, University of Arizona, Tucson, Arizona.

Lipman, P.W. 1984. Roots of ash flow calderas in western North America: windows into the tops of granitic batholiths. *Journal of Geophysical Research* 89: 8801-8841.

Marjaniemi, D.K. 1969. *Geologic history of an ash-flow sequence and its source area in the Basin and Range Province of southeastern Arizona.* Ph.D. dissertation, University of Arizona, Tucson, Arizona.

Pallister, J.S., E.A. du Bray, and J.S. Latta IV in press. Geologic map of the Rustler Park quadrangle, southeast Arizona. *U.S. Geological Survey Geologic Quadrangle Map GQ-1696.* scale 1:24,000.

Pallister, J.S., and E.A. du Bray, in press. Geologic map of the Fife Peak quadrangle, southeast Arizona. *U.S. Geological Survey Geologic Quadrangle Map GQ-1708,* scale 1:24,000.

Fig. 1. (next page) Geologic index map of the Chiricahua Mountains, after Marjaniemi (1969). Trc = Rhyolite Canyon Tuff; Tmr = moat rhyolite, Tdpi = dacite porphyry resurgent intrusion, Tdpl = dacite porphyry lava, T-pC = Tertiary to Precambrian basement rocks. Dense stipple pattern indicates pre-caldera Tertiary volcanic rocks, mostly rhyolite. Approximate structural boundary of the Turkey Creek caldera indicated by heavy line.


109 30 W
109°20
109° 10'
32° 00'
31° 50'
31° 40' N.
Cochise Head
ARIZONA
Pinery
Creek
Trc
Sugarloaf
Chiricahua Nat'l Mon
T-pC "basement"
Rhyolite moat lavas
Tmr
Fife
Vida
Buena Vista
Rustler Park
Trc
Tdpl
Dacite porphyry Tdpl
urkey Creek
Cave Creek
Portal
Silver
Centella Point
Cathedral Rock
Portal Pk
Pre -Trc rhyolite
Flys
Chiricahua
Snowshed
Rhyolite Canyon Tuff
Trc
Monte Vista
Tmr
Sentinel
Tmr
Tdpl
Sage
Horseshoe Cyn
Erickson
Rucker Cyn
Trc
Trc
ARIZONA
N
0 5 10km

GEOLOGICAL STRUCTURE OF THE CHIRICAHUA MOUNTAINS INFERRED FROM GEOPHYSICAL DATA

Mark E. Gettings
U.S. Geological Survey, University of Arizona, Tucson, AZ 85721

Introduction

Definition of geologic structures and delineation of the sequence of structural events in the southern Basin and Range province is a primary research goal of current U.S. Geological Survey investigations. Within this framework, the structural evolution of the "Sky Islands" in southeastern Arizona, including the Chiricahua Mountains, is an important project. Geophysical data are the primary source of information for the construction of models of the sub-surface geologic structure. The principal types of data used in this work are gravity (stemming from the variation in density of different kinds of rocks), magnetic field (variation in kind and content of magnetic minerals in rocks), electric and electromagnetic (variation in electrical resistivity of rocks), and seismic (variation in speed of sound propagation in different rocks). Seismic data are relatively expensive and difficult to interpret in mountainous terrain. The most commonly used structural interpretation tools are gravity and magnetic field data, supported when possible with electric and electromagnetic data. In southeastern Arizona, geophysical data in the mountain ranges are for the most part sparse, hence the current effort to collect and interpret data in the various ranges.

There are three basic sets of structures involved in the evolution of the Chiricahua Mountains. The first are structures mainly derived from the predominantly compressional mountain building event which ended approximately 70-65 My ago, deforming older marine sedimentary and volcanic rocks. This was followed by a mid-Tertiary (about 30?-20 Ma in the area of the Chiricahua Mountains) regional extensional event which stretched the crust in a northeast-southwest direction and led to the formation of metamorphic core complexes (such as the Santa Catalina-Rincon Mountains and the Pinaleno Mountains) and to the development of low-angle normal faults with displacements of as much as tens of kilometers. Finally, many penetrative high-angle faults developed whose offsets form the present Basin and Range topography. Estimates of age of this final event vary from 20 to 3 Ma, and it may have been sporadic. Structural features of the Chiricahua Mountains are a combination of these three major events, each of which overlaps somewhat both in time and space the previous event. A summary of the geologic relations of the Chiricahua Mountains may be found in Drewes (1981) and du Bray and Pallister (1991) and refererences therein. This report summarizes the results of efforts to date to create a generalized structural model of the Chiricahua Mountains.

Geophysical data

Geophysical data in the Chiricahua Mountains are sparse. Moss and Abrams (1985) presented gravity and aeromagnetic anomaly maps of the North End roadless area covering the region north from the Chiricahua National Monument. Other gravity data sources are the dataset of Lysonski and others (1980) and gravity data collected by the author in the Turkey Creek area. Aeromagnetic data along 5 km-spaced north-south lines at an altitude of 3 km are available in the dataset of Sauck and Sumner (1970). Aeromagnetic and gamma-ray spectrometric data have been acquired along 5 km-spaced north-south lines at a terrain clearance of 130 m (Texas Instruments, Inc., 1979). Audiomagnetotelluric soundings in the Onion

Saddle area and along Turkey Creek and Rock Creek are reported by Senterfit and Klein (1991). Paleomagnetic studies of the volcanic rocks of the Turkey Creek Caldera are summarized in du Bray and Pallister (1991). The discussion here will focus on the complete (terrain corrected) Bouguer gravity anomaly map of the Chiricahua Mountains area presented in Figure 1, although the structural interpretation in fact draws upon interpretations of all the available geophysical and geological data. Geographic locations shown for reference on Fig. 1 are: P, Portal; CH, Cochise Head; EP, Erickson Peak, and PM, Packsaddle Mountain. The locations marked with an "x" on Figure 1 are the gravity data points defining the map.

Discussion

The major features to be discussed are labelled on Figure 1. The dashed line enclosing a circular area and labelled TCC is the structural boundary of the Turkey Creek Caldera (du Bray and Pallister, 1991), the locus of the youngest ash-flow volcanism in the Chiricahua Mountains. The northwest trending Apache Pass Fault Zone, which has been an important structural control at least in Mesozoic and Tertiary times (Drewes, 1980), is labelled APFZ. A more diffuse northwest trending fault zone occurs in the southern Chiricahua Mountains and is here termed the southern fault zone, SFZ (Figure 1). In general, the local maxima of the gravity anomaly field (highs) correlate with areas of Cretaceous and older rocks which generally have a higher density than the mid-Tertiary rhyolites and the alluvial fill of the valleys. The local minima of the gravity anomaly field (lows) are marked by hachured contours and correspond mainly to the basins and areas of rhyolitic volcanism. However, detailed comparison of Figure 1 with the geologic map shows that the gravity anomaly also maps deeper structures beneath the volcanic and alluvial cover. For example, the marked increase to the south in the amplitude of the gravity anomaly low beneath the San Simon Valley (as the eastward projection of the APFZ, marked with a dashed line in Fig. 1, is crossed) implies that the valley fill is thickest to the south of the APFZ and that the fault zone was an active fault boundary in the formation of the valley. The gradients of the gravity anomaly field between highs and lows mark structural boundaries, either faults or contacts; steep gradients are due to sharp changes in the bulk rock density at shallow depths, whereas gentler gradients signify either sharp boundaries at greater depths between rocks of quite different density, or a more gradational change in density at any depth.

The northwest part of the Apache Pass Fault Zone is well defined by a gravity anomaly gradient (Fig. 1); the southeast part is less so, however there are few data points in the southeast to define the gravity anomaly field. Conversely, rocks separated by the APFZ in its southeast segment may have similar densities and thus a small or null gravity signature. As can be seen in Figure 1, the detailed definition of the shape of many of the anomalies is not possible with the existing data. Similar to the APFZ, the southern fault zone (SFZ, Fig.1) marks a boundary between intermediate anomaly values to the north and gravity anomaly highs to the south. This area marks the southeast terminus of a major northwest gradient zone in both the aeromagnetic (Sauk and Sumner, 1970) and gravity anomaly (Lysonski and others, 1980) maps. This structure may be a boundary between rocks of different terranes related to the compressional tectonic events ending in the early Tertiary. The strong gradient meandering from north to south along the east edge of the Chiricahua Mountains represents the range-front fault bounding the mountains and the San Simon basin (dashed line on Figure 1). There is not a similar feature on the west side of the mountains, suggesting that the block is not fault bounded on the west but instead is a tilt block, dipping down to the west beneath the Sulpher Springs valley. The central Chiricahua Mountains are predominantly mid-Terriary rhyolites, the youngest of which are associated with the Turkey Creek Caldera (TCC, Fig. 1). Existing data in the TCC area suggest that the caldera has a definite gravity low associated with it and detailed correlation of gravity anomaly values with the ash-flow tuffs and intrusive rocks of the TCC indicate that the intrusive rocks exposed in the Turkey Creek area are probably a thin sill with thickness on the order of 0.5 to 1 km rather than the top of a batholithic-size body.

Conclusions and further research

Structural modelling of the Chiricahua Mountains area based on gravity and aeromagnetic anomaly data and constrained by electromagnetic and geologic data indicate that the gross structure of the range is an approximately north-south trending, westward dipping fault block, whose westward boundary is outside the study area beneath the Sulpher Springs Valley. The east edge of the block, and indeed, the relative movements of blocks within the range, is controlled in part by older structures, parts of which have been reactivated in the tectonic events which uplifted the range. The collection of more gravity data and detailed magnetic survey data in the future will permit refinement of the model and testing of individual hypotheses regarding the timing and amplitude of movement of individual blocks.

Literature cited

Drewes, H.D., 1981. Tectonics of southeastern Arizona. *U.S. Geological Survey Professional Paper 1144,96* pp.

du Bray, E.A., and J.S. Pallister, 1991. An ash-flow caldera in cross-section: ongoing field and geochemical studies of the mid-Tertiary Turkey Creek caldera, Chiricahua Mountains, SE Arizona. *Journal of Geophysical Research,* v96, 13,435-13,457.

Lysonski, J.C., J.S. Sumner, C.L.V. Aiken, and J.S. Schmidt, 1980. Residual Bouguer gravity anomaly map of Arizona (IGSN71). *Department of Geosciences, University of Arizona, Tucson, Arizona,* scale 1:1,000,000.

Moss, C.K., and G.A. Abrams, 1985. Geophysical maps of the North End roadless area, Chiricahua Mountains, Cochise County, Arizona. *U.S. Geological Survey Miscellaneous Field Studies Map MF-1412-C,* scale 1:50,000, 2 sheets.

Texas Instruments, Inc., 1979. Aerial radiometric and magnetic reconnaissance survey portions of Arizona-New Mexico. *U.S. Department of Energy Grand Junction Office Report GJBX-223(79),* 7 vols.

Sauk, W.A., and J.S. Sumner, 1970. Residual aeromagnetic map of Arizona. *Department of Geosciences, University of Arizona, Tucson, AZ,* scale 1:1,000,000.

Senterfit, R.M., and D.P. Klein, 1991. Audiomagnetotelluric investigations at Turkey Creek Caldera, Chiricahua Mountains, southeastern Arizona. *U.S. Geological Survey Bulletin,* in press.

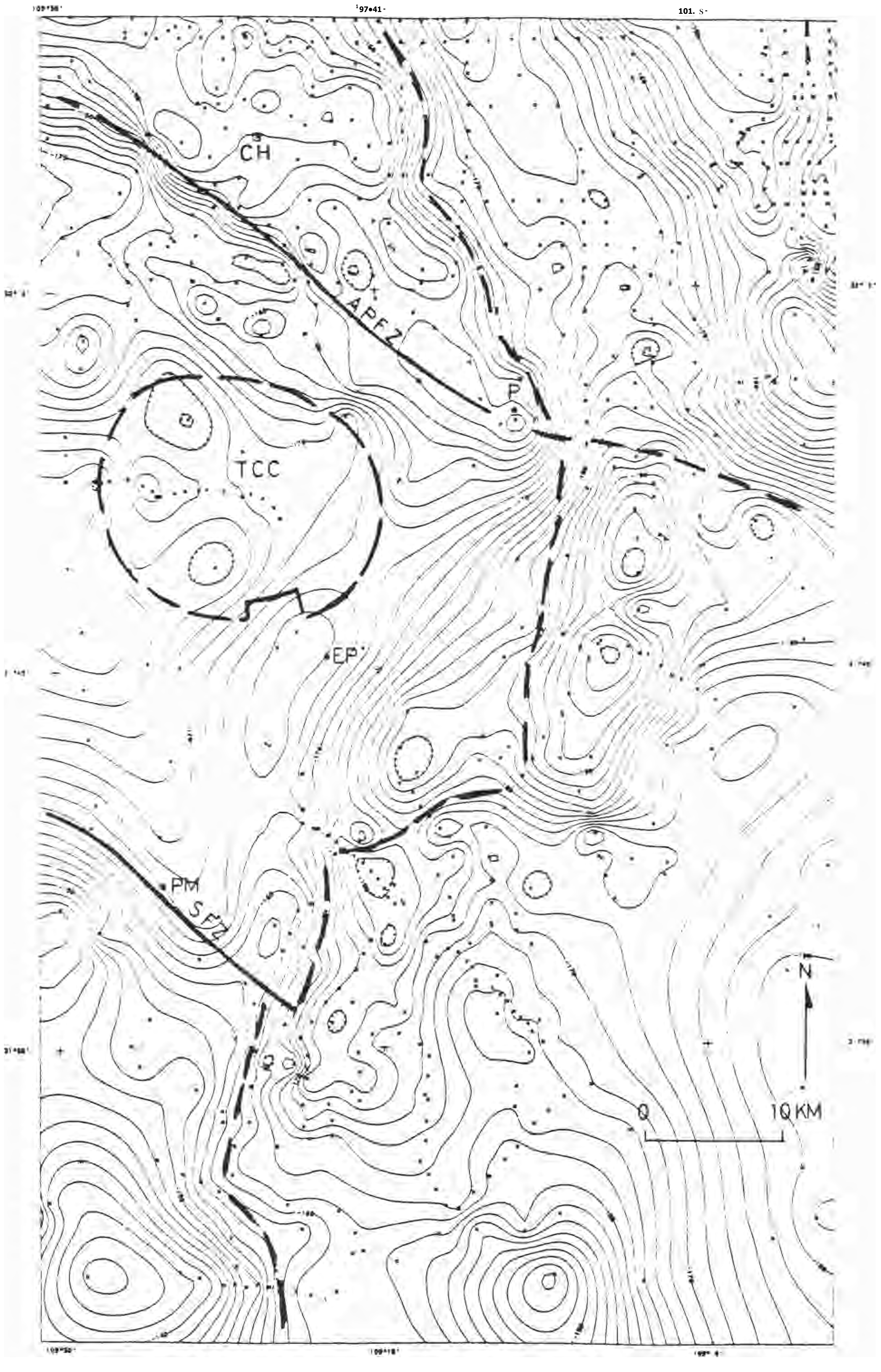


Figure 1. Complete Bouguer gravity anomaly map of the Chiricahua Mountains area, contour interval 2 mGal.

THE ECOLOGY OF FORESTS AND PLANTS IN THE CHIRICAHUA MOUNTAINS

FACTORS CONTROLLING PLANT DISTRIBUTIONS:
DROUGHT, COMPETITION, AND FIRE IN PINES IN THE CHIRICAHUA MOUNTAINS

Andrew M. Barton
Department of Biology, University of Michigan, Ann Arbor, MI 48109-1048
(current address: Center for Evolutionary Ecology, T.H. Morgan School of Biological Sciences,
University of Kentucky, Lexington, KY 40506)

Introduction

Ecologists have long been intrigued with how vegetation changes across the landscape. Such change is nowhere as obvious as in mountains in arid regions (e.g., Shreve 1915, Daubenmire 1943, Whittaker and Niering 1965). Vegetation zones along one mountain side are usually dependably repeated along other mountains sides in a region. Furthermore, elevational gradients of vegetation often resemble patterns found along other primary environmental gradients, such as latitude and soil type. These patterns suggest that similar forces control vegetation along the various natural continua that cause landscape variation in vegetation. Recently, bold models have been developed to explain how a small set of factors may control plant distributions and communities over such gradients. From 1986-1990, I addressed two of these models (Tilman 1988, Smith and Huston 1989) in a study of the factors controlling elevational distributions of pine species in the Chiricahua Mountains (see Barton 1991, 1992 and Barton and Teer 1992).

Soil productivity (i.e., plant productivity supported by soil) is closely correlated with elevation in many mountains such as the Chiricahuas. From lower to upper elevations, for example, I found that soil moisture increases and along with it vegetation cover and production increase substantially. As assumed by the models, I also found that with increasing soil productivity (i.e., elevation) , light available to seedlings decreased. The models propose that a tradeoff between tolerating limiting light availability and tolerating limiting soil resources, such as moisture, should result in changes in dominant species along such gradients of increasing soil moisture and decreasing light. The models predict that (1) shade tolerance and drought resistance should be negatively correlated among species, (2) limiting light (i.e., light competition) should control upper elevation limits of species distributions, and (3) limiting soil moisture should control lower elevation limits. However, I found that, with increasing elevation, fire frequency and litter depth also increased and soil temperature decreased. I tested the model predictions, and the role of these additional factors in controlling upper elevation limits. I focused on three pines: from lower to higher elevation, *Pinus discolor*, *P. leiophylla*, and *P. engelmannii* (following Bailey and Hawksworth 1983; see Figure 1), but included greenhouse work on two higher elevation pines.

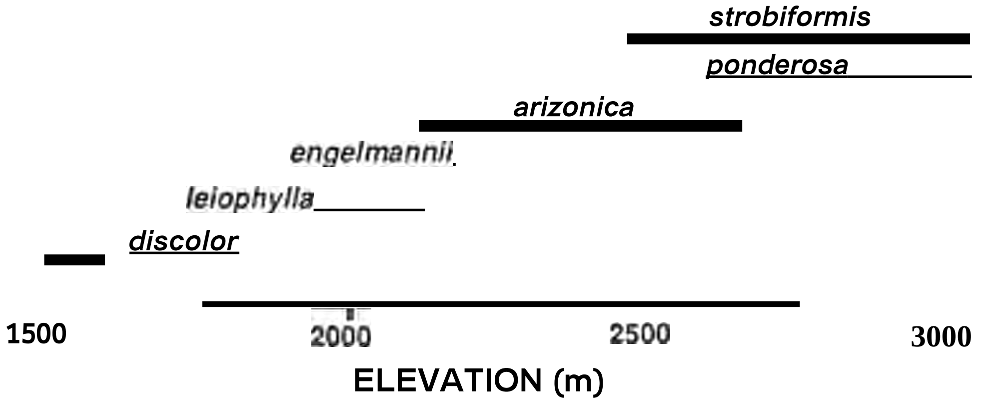


Figure 1. Elevational distributions of pine species in the Chiricahua Mountains.

The role of drought in controlling lower elevation limits

Consistent with the tradeoff hypothesis, three lines of evidence suggested that water stress strongly influenced lower elevation limits of all species. First, to examine species differences in drought resistance among the pines, I imposed a drought in a greenhouse on seedlings of five species that simulated field conditions at lower elevations during the dry season. As expected, lower elevation species exhibited better survival and photosynthesis (i.e., carbon dioxide uptake) than did upper elevation species.

Second, in a field experiment with the three focal pine species, hand-sown seeds of each species germinated with the summer rains in plots below their respective lower elevation limits, but all died by the end of the following May-June drought, apparently from water stress. In contrast, many seedlings from identical hand-sowing were still alive in experimental plots within and above each species' range after nearly two years. Finally, with decreasing elevation, naturally-occurring seedlings of the three species increasingly tended to occur in microsites with relatively low light, low soil temperature, and deep litter, all reflecting higher soil moisture compared to random microsites. Thus, near each species' respective lower elevation limit, water availability was apparently below the threshold for survival of its seedlings in all but the most mesic (protected) microsites.

Although natural recruitment, seedling survival, and seedling abundance were overall lower for each species near its lower elevation limit than elsewhere on the elevation gradient, height growth was, surprisingly, higher in these plots than anywhere else. Combined with the above results, this suggests that dry season water stress controls lower elevation limits by causing high mortality of young seedlings, rather than by curtailing germination or performance of older seedlings.

Most other experimental work has also supported the view that water stress and drought resistance control lower elevation limits of trees in western USA mountains (Daubenmire, 1943, Barnes and Cunningham, 1987). However, few studies have tested factors alternative to moisture availability that also correlate with the elevation gradient, such as high temperature, competition, and fire. For example, in an experiment on the small-seeded *P. leiophylla,* I found that this species' lower elevation limit was also influenced by a strong reduction in seedling emergence caused by the deep litter that uniformly occurred in the most protected, moist microsites under vegetation near its lower limit.

The roles of shade, litter, and temperature in controlling upper elevation limits

Inconsistent with the tradeoff hypothesis, upper elevation limits were not controlled by light limitation uniformly across species. In *P. leiophylla,* the middle elevation species, several lines of evidence did suggest that light limitation (i.e., competition for light) and deep litter control upper elevation limits. At higher elevations, seedlings tended to occur in microsites with higher light and lower litter depth compared to random microsites, whereas at lower elevations, this pattern was reversed. In a field experiment, *P. leiophylla* emergence and survival were significantly lower above its upper elevation limit compared to plots within its range, and removal of litter increased emergence and removal of canopy (and increase in light) increased seedling survival. Finally, in a greenhouse experiment, *P. leiophylla* was significantly less shade tolerant than several higher elevation pine species.

In contrast, in *P. discolor,* the low elevation species, low light, deep litter, and low soil temperature all appeared to be unimportant in controlling upper elevation limits. Emergence and survival were actually higher above its upper elevation limit than at middle elevations in the field experiment, whereas the other two species performed better at their middle elevation sites. Litter removal and canopy removal did not increase *P. discolor* emergence and survival, respectively, even above its upper elevation limit. In its highest elevation plots (i.e., near its upper limit), ***P.* discolor** seedlings actually occurred in microsites slightly lower in light, higher in litter depth, and equivalent in soil temperature to random microsites, contrary to expectations if these variables were limiting. Only the height growth rate of ***P.* discolor** appeared to be negatively affected by conditions at higher elevation. Finally, in greenhouse experiments, the very drought resistant ***P.* discolor** was, surprisingly, more tolerant of shade than higher elevation species, including ***P.* leiophylla**.

The role of fire in controlling the upper elevation limits of ***P.*** *discolor*

The above results raised the question of which other factors control the upper elevation limits of ***P.*** *discolor*. An early clue to this was the observation that fire incidence appeared to be substantially higher at elevations just above than within ***P.*** *discolor's* distribution. Two tests supported the hypothesis that these upper distribution limits are controlled, in part, by this higher incidence of fire. First, ***P.*** *discolor* exhibited slow juvenile growth rates, thin bark, and other traits suggesting a lack of fire resistance compared to the two pine species occurring at higher elevations than ***P.*** *discolor*. Second, in two wild fires, survival of ***P.*** *discolor* was significantly lower than that for the other two species. This conclusion is corroborated by the observation that juvenile ***P.*** *discolor* up to nearly 50 yrs old occurred commonly at much higher elevations than did adults, in plots with very low light and soil temperature levels and very deep litter. This pattern is likely a result of fire suppression over the past 75 years. Before suppression, frequent fires (see Swetnam et al. 1989) probably excluded the fire-sensitive ***P.*** *discolor* from elevations above its current adult distribution. Suppression of fire has so reduced fire incidence that ***P.*** *discolor* juveniles have begun to invade these areas. Whether this species could ever attain numerical dominance in these sites is unclear (see Barton 1992).

Conclusions and further research

The lack of a tradeoff between tolerance of limiting light versus limiting soil moisture in these species may result from (1)P. *discolor's* large animal-dispersed seeds and its strategy of exploiting nurse tree sites at low elevation and (2) the apparent fire-associated regeneration of the other two pine species focused on here. Nevertheless, there may still be important tradeoffs in this system between success at low versus higher elevations: constraints imposed by drought resistance on the maximum growth rate and height of ***P.*** *discolor* may limit this species' fire resistance and its ability to prosper in the moister but more fire-prone higher elevations. The divergent ecological strategies of the three pines correspond closely to a recent classification of strategies in pines and appear to be strongly correlated with phylogeny (McCune 1988), suggesting that these suites of traits occur commonly in pines.

It is important to emphasize that the importance of fire in the distributions of pines in the Chiricahuas rests on the cause-and-effect relationships between fire and the environment: with increasing elevation, soil moisture, and fuel load, fire incidence increases, at least over the lower half of the elevation gradient studied here. Such correlations between soil resource gradients and fire appear to be ubiquitous in nature. These results suggest that fire, or other agents of selective mortality correlated with productivity, can exert strong control over plant distributions and community composition, and should be incorporated into general models relating plant strategies to community structure.

Before European settlement of the southwest, fire occurred frequently in the Chiricahua Mountains and nearby mountains (e.g., Swetnam et al. 1989). Because of its far-reaching effects on light, nutrients, and water and on plant survival and growth and because plant species differ in their ability to tolerate and exploit these results, fire probably played a central role in controlling not just plant distributions but all aspects of the ecology of plant populations, communities, and ecosystems in the Chiricahuas. In so far as animal populations depend on or are associated with vegetation, this statement probably also applies to animals. Given that ecologists have only recently turned their attention to the ecological role of fire in southeast Arizona, there is great need for research that integrates the role of fire with other factors controlling communities and ecosystems in this region and applies this knowledge to the management and conservation of these systems.

Literature Cited

Bailey, D. K. and F. G. Hawksworth. 1983. Pinaceae of the Chihuahuan Desert Region. Phytologia 53: 226-234.

Barnes, F. J. and G. L. Cunningham. 1987. Water relations and productivity in pinyon-juniper habitat types. Pages 406-411 in R. L. Everett, editors. Proceedings--Pinyon-Juniper Conference. United States Department of Agriculture Forest Service, Intermountain Research Station General Technical Report INT-215.

Barton, A. M. 1991. Factors controlling the elevational positions of pines in the Chiricahua Mountains, Arizona: drought, competition, and fire. Ph.D. dissertation. University of Michigan, Ann Arbor, MI, USA.

Barton, A. M. and J. A. Teeri. 1992. The ecology of elevational positions in plants: drought resistance in five montane pine species in southeast Arizona. American Journal of Botany, in press.

Barton, A. M. 1992. Factors controlling plant distributions: drought, competition, and fire in montane pines in the Southwest. Ecological Monographs, in review.

Daubenmire, R. F. 1943. Vegetation zonation in the Rocky Mountains. Botanical Review 9: 325-393.

McCune, B. 1988. Ecological diversity in North American pines. American Journal of Botany 75: 353-368.

Shreve, F. 1915. The vegetation of a desert mountain range as conditioned by climatic factors. Publication No. 217, Carnegie Institution of Washington, Washington, District of Columbia, USA.

Smith, T. and M. Huston. 1989. A theory of the spatial and temporal dynamics of plant communities. Vegetatio 83: 49-70.

Swetnam, T. W., C. H. Baisen, P. M. Brown, and A. C. Caprio. 1989. Fire history of Rhyolite Canyon, Chiricahua National Monument. Report to Chiricahua National Monument, National Park Service, United States Department of the Interior.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Monographs in population biology, No. 26. Princeton University Press, Princeton, New Jersey, USA.

Whittaker, R. H. and W. A. Niering. 1965. Vegetation of the Santa Catalina Mountains, Arizona: II. A gradient analysis of the south slope. Ecology 46: 429-452.

FACTORS AFFECTING PLANT SPECIES RICHNESS IN THE MADREAN ARCHIPELAGO NORTH OF MEXICO

Peter S. Bennett
Michael R Kunzmann
Cooperative National Park Studies Unit, Univ. Arizona, 85721

Introduction

The mountains of the Madrean Archipelago (Lowe 1991) support a rich and diverse biota. The Chiricahua Mountains, for example, cover only 0.5% or 157,000 hectares out of 29 million in Arizona, yet 30% of the Arizona flora and nearly 50% of all bird species north of Mexico are found here. Three major floral Pliocene-Pleistocene segregates of the Arcto-Tertiary and Madro-Tertiary geofloras inhabit these mountains and their surrounding pediments: (1) a northern element (forest and tundra) at higher elevations; (2) a younger (woodland and chaparral) mixed southern element at middle elevations; and (3) the deserts, which are very young, on the mountain pediments (Axelrod 1958, Lowe 1964). This agglomeration of floral elements makes high species diversity possible. McLaughlin (1986) presented statistical data depicting the distribution of the Madrean and other floristic elements of Southwestern vegetation. He shows the summer wet Madrean forest and woodland segregated from the winter wet Great Basin, Colorado Plateau, Mohavian, and other elements of the West.

This richness of plant species of the Madrean Archipelago has been remarked upon recently by Bowers and McLaughlin (1982). They examined data from a number of local floras and applied multiple regression analysis to estimate species numbers (=gamma diversity [Whittaker 1972]). Elevation and collection effort were the best predictors of diversity (R^2=0.77) but areal extent was less important.

Brady (1973) and Wentworth (1985) suggested that the scattered Madrean woodland canopy creates a heterogenous environment supporting a number of herbaceous species. Bowers and McLaughlin (1982) identified three factors associated with richness: (1) Madrean vegetation and the vegetation belt between the Madrean woodland and chaparral and the upper portion of the semi-desert grassland; (2) aquatic habitats; and (3) canyon environments.

Large absolute species diversity of Madrean floral elements, compared with others, indicates an evolutionary history distinct from the balance of the montane West. Our intent is objective examination of this distinctness and species richness.

Methods

Bennett, Johnson, and Kunzmann (in prep.) assembled an annotated checklist of the floras of the Chiricahua, Animas, Pinaleno, Rincon, Santa Catalina, and Sierra Ancha mountain ranges that furnished these data: species name, elevational range, community association, and distribution. Life form, growth form, and floral element (areal type) conforming to Whittaker and Niering (1964) were also included in the list.

We measured terrain roughness (canyon and ridges) on topographic maps by using line transects drawn along the crest and at right angles to the crest of each mountain range, calculating absolute elevation change divided by distance. We call this attempt to quantify canyon habitat prevalence a roughness index (RI). Pearson's product moment was used to correlate RI with floral richness.

Bowers and McLauglin's (1982) equations for predicting relative species diversity and Otsuka's index of diversity (given by Simpson 119801) were calculated for each range included in our plant list. We performed cluster analysis (Wilkinson 1990), using Bowers and McLauglin's relative species diversity, Whittaker and Niering's floral elements, and Otsuka's index. Euclidean distance and complete linkage were used for clustering.

Results

The Chiricahua and Animas floras had the highest proportion of Madrean vegetation while the Pinaleno and Sierra Ancha had the lowest. The Chiricahua had the larger flora (1188 species) but the Animas had the greater proportion of Madrean species within its smaller flora (Table 1). Cluster analysis of floral composition of the Animas and Chiricahua mountains indicates floral similarity and a high degree of Madreaness (Fig. 1). The Pinaleno and Sierra Ancha cluster on the basis of western and northern floral elements. Lower Madreaness of the Sierra Ancha is explained, in part, by a winter precipitation pattern more prevalent there than in the other ranges.

Cluster analysis of all floral elements combined, displays the mountain ranges in geographical proximity as well as in floral affinity, probably indicating overall floral similarity based on geographical proximity, as expected. However, clustering on the Madrean floral element alone, shows floral similarities mostly unrelated to geography. While the Chiricahua and Animas mountains remain closely connected, the others do not. The geographically close Catalina and Rincon mountains are more distantly clustered than are the Catalina and Pinaleno mountains seemingly indicating that Madrean relationships are less geographically controlled than are other floral elements (Fig. 1).

Analysis of the floral similarity using Otsuka similarity index (IS) verifies cluster analysis results. Chiricahua/Animas = 0.720; Chiricahua/Ancha $OI_{Maorean}$ = 0.585; Animas/Ancha $OI_{Maarean}$ = 0.528. Otsuka indicies for endemics tend to be lower, i.e., Chiricahua/Ancha = 0.315; Animas/Ancha = 0.174. The Chiricahua/Animas have a high index of similarity while Chiricahua/Ancha and Animas/Ancha are lowers.

The Bowers & McLauglin species richness predictions are positive for strongly Madrean ranges (Chiricahua, Animas, Catalina, and Rincon mountains) indicating greater than expected diversity but negative for those with cosmopolitan western montane elements (Pinaleno and Sierra Ancha), indicating less diversity than expected (Table 1).

Roughness index (RI)—elevation change per horizontal unit— ranges from a low of 0.144 in the Sierra Ancha to 0.503 in the Animas Mountains (Table 1). Percent of Madrean flora and RI are highly correlated ($R^2 = 0.897$).

Conclusions

Madrean plant species richness in southeastern Arizona, and perhaps in northern Mexico, is higher than expected empirically and analytically. Of the Madrean Archipelago ranges in the United States, the Chiricahua Mountains and Animas Mountains have the highest percentage of Madrean Evergreen Forest and Woodland species and higher than expected floral richness. The disparity between physical proximity and Madrean vegetation similarity may indicate that factors other than geography control Madrean relatedness. Low relatedness of endemic species within the archipelago may reinforce this idea. The ranges in the archipelago may be recently isolated following a long period of floristic connection during Tertiary and Quaternary periods.

Lesser species richness of the Madrean vegetation in the winter wet climate of the Sierra Ancha is an indication that Madrean vegetation is ecologically dissimilar from that of montane west. Strong correlation between RI and species richness may be indicative of vegetation development on ranges with variable slopes and aspects and especially ones with many drainages (canyon environments).

Compared with Rocky Mountain, Sierran, or Cascadian ecosystems, the Madrean is the least understood. Application of western montane management paradigms to species- rich Madrean communities about which we know little may be unwarranted. Further research into autecology, community structure (especially of woodlands), evolution of the Madro-Tertiary Geoflora, and habitat structure are clearly needed.

Literature Cited

Axelrod, D.I. 1958. Evolution of the Madro-Tertiary Geoflora. Bot. Rev. 24:433-509.

Bennett, P.S., M.R. Kunzmann, and R.R. Johnson. In prep. An annotated checklist of the vascular plants of Chiricahua Mountains including Chiricahua National Monument Fort Bowie National Historic Site and species from the Sierra Ancha, Pinaleno Mts., Santa Catalina Mts. and Rincon Mts.

Bowers, J.E. and S.P. McLaughlin. 1982. Plant species diversity in Arizona. Madrono 29:227-233.

Brady, W. 1973. Pattern of vegetation diversity in the Huachuca Mountains. Ph.D. dissertation, Colo. State Univ., Fort Collins.

Lowe, C.H. 1964. Arizona landscapes and habitats. Pages 1-132 in C.H. Lowe (ed). The vertebrates of Arizona; with major section on Arizona habitats. Univ. Ariz. Press, Tucson.

Lowe, C.H. 1991. On the biogeography of herpetofauna at Saguaro National Monument, Arizona. In L Bellantoni, (ed). Symp. Res. Saguaro Nat. Mon.; January 23-24, 1991, Tucson, Ariz.

McLaughlin, S.P. 1986. Floristic analysis of the southwestern United States. Great Basin Nat. 46:46-65.

Simpson, G.G. 1980. Notes on the measurement of faunal resemblance. Amer. J. Sci 258A:300-311.

Wentworth, T.R. 1985. Vegetation on limestone in the Huachuca Mountains, Arizona. Southwest. Nat. 30:385-395.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon 21:213-251.

Whittaker, R.H. and W.A. Niering. 1964. Vegetation of the Santa Catalina Mountains, Arizona. I. Ecological classification and distribution of species. J. Ariz. Acad. Sci. 3:9-34.

Wilkinson, L. 1990. SYSTAT: the system for statistics. Evantson, Il.

Table 1. Selected Floral Statistics for Madrean Archipelago North of Mexico

Range[1]	Species observed	Species percent of est.[2]	Area (ha) x1000	Elev. max.	Madrean percent[3]	Roughness index
Chiricahua	1199	27.5	157.3	2987	18.0	0.275
Animas	663	2.5	79.9	2586	19.8	0.503
Catalina	843	0.2	102.3	2792	12.7	0.206
Cat+Rincon[4]	1128	34.0	179.0	2792	13.3	0.192
Rincon	864	11.8	76.7	2594	13.5	0.165
Pinaleno	834	-7.2	88.9	3266	12.6	0.210
S. Ancha	705	-9.3	200.2	2175	11.8	0.144

1. Ranges selected on the basis of having completed floras.
2. Predicted species (peroentage greater or less than observed [Bowers & McLaughlin 19€2]).
3. Percentage of flora with Madman affinity (Whittaker & Niering 1964).
4. Floras of Santa Catalina and Rincon mountains combined (= Boolian AND).

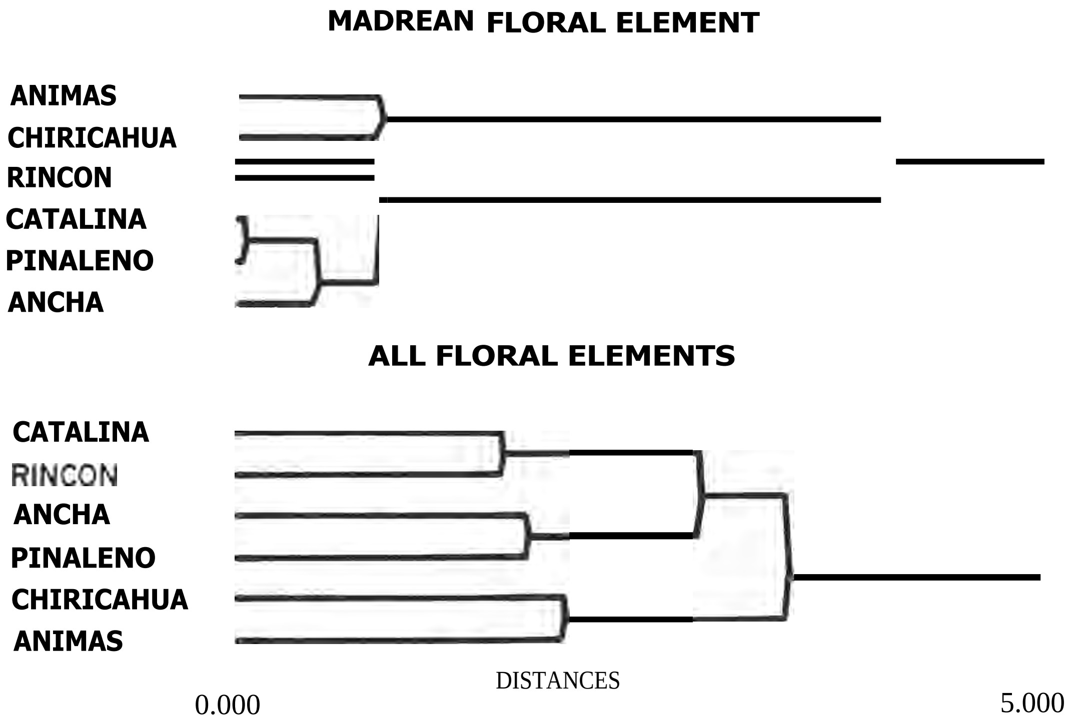


Fig. 1. Dendrograms of inter-range floral relatedness. The top diagram depicts the Animas and Chiricahua as closely related by the Madrean floral element. The other ranges are mixed without relationship to geographical positior.. Linkage by all floral elements (lower diagram), more nearly represents geographical closeness. Madrean relatedness is, therefore, not simply a geographical function.

SENSITIVE PLANT STUDIES IN THE "SKY ISLAND" MOUNTAIN RANGES OF S.E. ARIZONA

David Gori
The Nature Conservancy, Arizona Chapter
Tucson, AZ 85705

The Nature Conservancy is an international, non-profit organization whose goal is to protect biodiversity globally. It works by identifying and protecting habitat for endangered species and biotic communities as well as cooperating and sharing information with federal and state agencies to protect and manage endangered species and communities on public lands. The Conservancy manages 11 preserves in Arizona, two of which are managed cooperatively with public partners. One of its preserves, the Portal Preserve, is located along Cave Creek in the Chiricahua Mountains, downstream from the Southwestern Research Station and the Coronado National Forest boundary. The preserve is 40 acres in size and is a combination of Conservancy-owned and private land that is protected by conservation easements. The mixed broadleaf deciduous forest along Cave Creek supports peripheral populations of Mexican birds, mammals, and reptiles, native fish (Rhinichthys osculus) and globally threatened species such as Sanborn's Long-nosed bat (Leptonycteris curosoae verbabuenae) and the Chiricahua Leopard frog (Rana chiricahuensis).

The Nature Conservancy is cooperating with the Coronado Forest on a study of rare plant species that occur on the mountain islands of s.e. Arizona and northern Sonora. With approximately sixty rare and/or sensitive plants, the Coronado Forest has among the largest number of rare plant species of any national forest in the United States; most of these species are candidates for federal listing as threatened or endangered species by the U.S. Fish and Wildlife Service. Prior to the initiation of this study in 1988, we lacked basic information on the ecology and status of most of these species and little was known about the distribution of these species in Mexico. Thus, the purpose of the study was threefold: first, to assess the current distribution of target plant species by revisiting historic locations and surveying appropriate habitat in Arizona and Sonora; second, to establish monitoring plots in order to determine population trends and to measure basic demographic parameters including recruitment and size-specific rates of growth, survivorship, and reproduction; and, third, to identify potential threats to the populations and make recommendations to improve species' management.

The target species are listed in Table 1 along with their distribution in the United States and the habitats they occupy. Most species occur in a restricted number of mountain ranges, even though appropriate habitac presumably exists in other ranges where they do not occur. In addition, most of the target species occupy "insular" habitats within their geographic range which may explain their rarity and patchy distribution (if dispersal capabilities are limited). Some of the rare species, however, occupy what appear to be common, widespread habitats suggesting that poor dispersal capabilities or stringent germination requirements may limit their distributions. The study has resulted in a great deal of information on the ecology, demography, and distribution of these species in the U.S. and Mexico. A significant number of new populations have been located, in some cases increasing the number of localities by 2 or 3 times. However, we are convinced on the basis of extensive surveys that many of these species are indeed rare.

Population size trends and threats facing populations are summarized in Table 2. Most populations are stable, however, a small number are increasing or decreasing in size. Furthermore, populations and species face a variety of threats including recreation, floods, and grazing and trampling by cattle. Species that occur in mesic understory habitats (e.g., E. *plummerae* and S. *huachucanus*) and moist canyon bottoms (e.g., A. *grandiflora* and L. *parryi*) are particularly vulnerable to catastrophic fires that result from unnaturally high fuel buildups and poor watershed conditions that result from grazing and fire suppression. Catastrophic fires remove the tree canopy, changing moisture conditions for plants growing in the understory, and increase surface runoff following rains, resulting in scouring floods. Protective management for these species should include prescribed burns to reduce accummulated fuel loads and improved grazing management to increase herbaceous/grass vegetative cover in watersheds.

Population monitoring should continue on the above species and demographic studies and threats-assessment initiated for other rare plants species that occur on "sky island" mountains of the border region. Future research should focus primarily on the species that show declining populations or large fluctuations in population size. Information needs include: (1) studies to assess genetic variation within and between populations in order to prioritize conservation efforts and design recovery programs (Genetic studies on two rare species, *Rumex orthoneurus* and *Lilium parryi*, have already been completed); (2) experiments to determine the germination requirements of target species; and (3) studies to assess the effect of prescribed burns on recruitment, survivorship and reproduction for species that may benefit from fuel load reductions or that occupy habitats previously subject to frequent natural fires.

Table 1. The distribution and habitat of rare plant species in the borderlands region monitored between 1988 and 1991.

SPECIES	HABITAT	MTN. RANGE
Amsonia grandiflora	Canyon bottoms	Patagonia, Atascosa S. Cibuta, S.los Ajos
Euphorbia plummerae	Canyon bottoms	Huachuca, Santa Rita Patagonia, S. Madre
Dalea tentaculoides	Canyon bottoms rocky hillsides	Atascosa, Quinlan
Astragalus cobrensis var. maguirei	Canyon bottoms	Chiricahua,Pelncillo
Lilaeopsis schaffneriana ssp. recurva	Small streams	Huachuca, Patagonia
Lilium parryi	Stream banks	Huachuca, Sta Rita, Chiricahua
Rumex orthoneurus	Montane cienega, stream	Chiricahua, Huachuca Penaleno
Talinum marginatum	Rock terraces	Huachuca, S. Los Ajos, S. San Luis
Cheilanthes arizonica	Rock faces, cliffs	Huachuca, Mule Chiricahua, S. Madre
Draba standleyi	Rock faces, high elevation	Chiricahua
Erigeron kuschei	Rock faces, high elevation	Chiricahua
Erigeron lemmoni	Cliffs	Huachuca
Polemonium pauciflorum var. hinckleyi	Montane talus, streamside	Chiricahua, Davis (TX)
Senecio huachucanus	Montaine stable talus:pine/oak	Huachuca, Sta Rita S. Azul
Astragalus hypoxylus	Limestone soil, Oak woodland	Huachuca, Patagonia
Phaseolus supinus	Grasslands oak/mesquite	Patagonia, Atascosa S. Cibuta
Agave parviflora ssp. parviflora	Grasslands, oak savanah	Atascosa, Patagonia Sta Rita, S. Cibuta

Table 2. A summary of population size trends and threats facing target rare plant species. The number of populations and duration of monitoring is also given. Stable population size = (S); Declining population size = (D); and Increasing population size = (I).

Species	**Years Monitored**	**No. Pops.**	**Trend**	**Threats**
Amsonia grandiflora	**4**	**4**	**S**	**Recreation** **Floods** **Grazing**
Euphorbia plummerae	3	2	S	Floods
Senecio huachucanus	3	2	S	Wildfires
Dalea tentaculoides	2	1	S	Grazing
Erigeron lemmoni	3	1	S	**None**
Phaseolus supinus	2	1	S	None
Lilaeopsis recurva	3	6	S,I	Floods
Lilium parryi	4	7	I,D	Floods Herbivory
Astragalus hypoxylus	4	3	S?,D	Drought Herbivory Recreation Grazing
Talinum marginatum	4	2	D	Roads/ trails
Cheilanthes arizonica	1	1		None

THE DISTRIBUTION AND ECOLOGY OF FOUR RARE PLANT SPECIES FROM THE CHIRICAHUA MOUNTAINS, ARIZONA

James Malusa
Department of Ecology and Evolutionary Biology
University of Arizona, Tucson 85721

Introduction

Sixty-one species of plants in the Coronado National Forest are recognized by the U.S. Forest Service as "sensitive" because they have either a limited or a poorly understood distribution. Twelve of these sixty-one are found in the Chiricahua Mts. of southeastern Arizona. To better understand their ecology and potential threats to their persistence, the Nature Conservancy and the Coronado National Forest jointly funded a study of four of these sensitive species: Astragalus cobrensis var. maguirei, Draba standleyi, Rumex orthoneurus, and Polemonium *pauciflorum* var.hinckleyi. Of particular interest was Rumex orthoneurus , a Catagory 1 Canidate (U.S. Fish and Wildlife) Endangered Species, and the subject of a Coronado National Forest transplanting program, to extend its range to new areas in the Chiricahuas.

Results and Discussion

The major observations concerning the ecology and distribution of the sensitive plant species are summarized below. For a more extensive account of surveys and monitoring of sensitive plants in the Coronado National Forest in 1991, see Malusa et. al. (1992).

Astragalus cobrensis var. maguirei - (Family Leguminosae) - This variety is known from the northeastern Chiricahua Mts. of Arizona, with some putative outliers in the Peloncillo Mts. in far southeastern Mountains A. cobrensis var. maguirei is found between approximately 5,000 and 7000 feet. It is associated with pinyon/alligator juniper/mixed oak at lower elevations, and Apache pine/ponderosa pine/Douglas fir at higher elevations. Typically it grows along canyon bottoms, often in the steep banks cut by the stream. At lower elevations it appears restricted to near the canyon bottom, while at higher elevations it may be found not in association with canyon bottoms, but rather in leaf litter on shady slopes. It prefers open shade, although it will grow in full sun if in a fairly mesic site.

A new and extensive population was found along West Turkey Creek in the Chiricahua Mountains. Over 500 individuals were counted, and the total population in the canyon is likely several thousand. Formerly known only from canyon bottom habitat, *A. cobrensis* var. *maguirei* was found growing on north-facing slopes at up to 7000 ft. in the understory of douglas fir. Another new location was from Guadalupe Canyon near Guadalupe Spring in the Peloncillos, where 60 individuals were found. Other surveys in the Chiricahuas censused known populations in Pinery, Bonita, and East Whitetail Canyon, while surveys in Rucker Canyon, Clanton Draw, and Sycamore Canyon revealed no new populations.

Draba standleyi (Family Cruciferae). *D. standleyi* is found from 6000 to 9400 ft, from the Davis Mts. of southwestern Texas, the Organ Mts. of New Mexico, to the Chiricahua Mts. of southeastern Arizona. In the Chiricahua surveys, *D. standleyi* was almost always found on mesic, north-facing cliffs and other large rock exposures at high elevations, where it is often associated with *Erigeron kuschei,* another Forest Service Sensitive species. Other common associates are *Heuchera versicolor* and *Geranium richardsonii.* At some sites, such as 9375 foot Paint Rock in the Chiricahuas, *D. standleyi* is completely restricted to the north-facing cliff faces, while nearby south, east and west exposures will hold *Draba helleriana* or *D. petrophila.*

Further, it appears that *D. standleyi* requires not only north-facing rock, but a relatively large rock also, since it was (almost) never found on stable boulders in cool, sheltered locales. Most plants were on rock faces with a surface area of at least 20 square meters. This may be because the separate populations of *D. standleyi* are broadly scattered and uncommon, and minor perturbations may eliminate a small population. To be reestablished requires colonization from a distant source of *D. standleyi.*

An exception to the "north-face only" rule is at the 9300 ft. Centella Pt. in the Chiricahuas, at the site of a three-year old burn. Where the burn was of low intensity, sparing the overstory, there are *D. standleyi* at the margin between the burnt-needle covered forest floor and the rocky cliff edge that drops off steeply to the southeast into Cave Creek. Douglas fir and southwestern white pine are just over and to the north of the *Draba,* while the more arid-adapted *Holodiscus* and *Echinocereus are* just south at the cliff's verge. Along with the *Draba* are the common colonizers *Achillea lanulosa* (milfoil) and *Verbena bipinnatifida,* and the Forest Service Sensitive species *Polemonium pauciflorum* subsp. *hinckleyi.*

The surveys located four new populations in the Chiricahua Mts: Paint Rock, Bootlegger Trail, Centella Point, and at the head of Winn Falls. These surveys showed that *D. standleyi* is limited to the north faces of cliffs at high-elevation, with the exception of the Centella Point population, which was in an area that had experienced a low-intensity burn three years earlier; there, it grew in needle litter beneath an overstory of douglas fir and white pine. Other surveys relocated an historic population in East Turkey Creek, and failed to find any populations in the Pinaleno Mts.

***Polemonium pauciflorum* subsp. *hinckleyi* -** (Family Polemoniaceae). Subspecies *hinckleyi* is found from the Davis Mountains of southwestern Texas, the mountains of northern Mexico, and in the Chiricahua Mountains of Arizona, from 5000 feet to 11,500 feet (the latter in Nuevo Leon, Mexico). This distribution is similar to that of *Draba standleyi.*

No other *Polemonium* occur in the Chiricahua Mts., although *P. foliosissimum* is common in the nearby Pinalenos and other high mountains. The ecology of subspecies *hinckleyi* is something of an enigma, as it is found in a variety of habitats, yet still uncommon. In the Chiricahua Mountains it was found in the rubble at the edge of a dirt road in open shade, (near Barfoot Park), on north-facing talus slopes (Bootlegger Saddle and Centella Point), in open shade in a recent burn area (Centella Point) and along a creek (Rock Creek). The only common denominator appears to be some form of disturbance. However, there are an abundance of disturbed sites that appear entirely appropriate, but that hold no subsp. *hinckleyi.*

Because this species was at the burn site at Centella Point, it's possible it was more common when low intensity burns were more common in the forest. However, some areas, such as the south-facing slope of Raspberry Peak, showed evidence of low intensity burns relatively recently, and yet had no *Polemonium.*

About 200 plants were located at four new sites in the Chiricahua Mts. (Bootlegger Trail, Centella Point (two sites), and along Rock Creek. Surveys in the Pinalenos revealed no populations.

Rumex orthoneurus* -** (Family Polygonaceae). ***R. *orthoneurus* prefers moist, organic soils near springs or streams, at elevations from 6500 to 9000 feet. In general, it is found in "low-energy" mesic locations, near the heads of creeks, where flooding events are relatively rare. When found further downstream, it is usually behind rocks and logs that shelter it from floods.

Typically, ***R.*** *orthoneurus* is found with false-hellebore *(Veratrum californicum),* cow parsnip *(Heracleum lanatum)* and a variety of sedges and rushes. *Iris missiuriensis* is often found in the slightly drier meadows surrounding the springs.

A taxonomic study of the angle between the midvein and lateral vein in the leaf (see Malusa et al. 1992) showed that the populations of *Rumex* in southeastern Arizona differ significantly from the populations in the White Mountains; this finding lends credence to the distinction between *R. orthoneurus* and *R. occidentalis.* The study sampled 9 to 12 plants from each of eight populations of *Rumex..*

Herbarium records from the University of Arizona have identified the populations from the Chiricahua, Sierra Ancha, Pinaleno (Hospital Flat), Huachuca and Escudilla Mt. (near the White Mts.) as *Rumex orthoneurus.* The results of the taxonomic study indicate that the Escudilla Mt. population is probably *R. occidentalis.* Because each population shows a range of variation in the leaf lateral vein angle, the single specimen at the University from Escudilla Mt. (ARIZ 281508) was "misidentified" only because it is a single specimen that happened to be similar to other populations of *R. orthoneurus.*

The Coronado's Management Plan for *Rumex orthoneurus* (Douglas Ranger District, # 2670, Oct. 1989) details the numerous locations where transplants or seeds were placed in an effort to bolster the population. These sites were relocated and surveyed in 1991, and all *Rumex* censused and photographed. Populations of 24 to 34 plants have taken at Cima Creek, Tub Spring, and near the site of the sawmill at the head of East Turkey Creek. At Barfoot Park and below Rustler Park, there are over two hundred plants. Transplants at Barfoot have done well inside the enclosure, but occasionally suffer from grazing by cattle. The population below the lower Rustler Spring enclosure, along a fork of East Turkey Creek, is doing very well, probably because of the reliable "source" population within the enclosure.

Literature cited

Malusa, J., D. Gori, P. Warren, E. Saucedo. 1992. Population studies of sensitive plants of the Coronado National Forest. A report submitted by The Arizona Nature Conservancy to the Coronado National Forest.

STUDIES IN THE MYCOFLORA OF THE CHIRICAHUA MOUNTAINS, COCHISE COUNTY, ARIZONA, U.S.A. I. PRELIMINARY REPORT ON SPECIES DISTRIBUTION, ECOLOGY, AND BIOGEOGRAPHICAL AFFINITIES

F. H. Nishida[1], W. J. Sundberg[2], J. A. Menge, J. S. States, R. E. Tulloss[5], J. Cifuentes Blanco[6]

Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA 90007; [2] Dept. of Plant Biology, Southern Illinois University, Carbondale, IL 62901; Dept. of Plant Pathology, University of California, Riverside, CA 92521; Dept. of Biology, Northern Arizona University, Flagstaff, AZ 86011; P.O. Box 57, Roosevelt, NJ 08555-0057; [6] Herbario, Facultad de Ciencias, Apartado Postal 70-399, UNAM, Coyoacan 04510, Mexico D.F., Mexico.

INTRODUCTION

The compact nature of the Chiricahua Mountains, their heights reaching nearly 3000 m, and their several distinct biomes from Sonoran desert to montane conifer forest offer a unique opportunity to explore the dynamics of fungal ecology, such as species distribution, diversity, habitat preference, fruiting patterns and relative abundance. With rugged and varied topography and isolation from other forests by desert—comprising a "sky island"—they offer the possibility of finding rare or endemic species. Understanding the mycoflora of the Chiricahua Mountains, a region spared extensive glaciation and providing relict conifer montane forests, would enhance paleo-botanical knowledge and add to understanding of biotic communities of the Southwest. Furthermore, many agarics are obligatorily symbiotic (mycorrhizal) with certain plants, while other fungi are specifically saprophytic or parasitic. Hence, information on their occurrence is applicable to studies ranging from evolution to systems ecology.

Fungi of the Aphyllophorales (wood-rotting Basidiomycetes) throughout Arizona and their interactions with insects (Gilbertson, 1984) have been well documented by Gilbertson (1974, 1981; Gilbertson & Ryvarden, 1986-1987). Hypogeous fungi of the Southwest are recorded by States (1983,1984) and Fogel & Pacioni (1989); mycophagy by small mammals of hypogeous fungi was reported by Fogel & Trappe (1976) and States (1990). Boletes of the Southwest were reported by Thiers (1976). Published studies on agarics of the Southwest are scarce, outside of a recent guide treating common species (States, 1990). Ecosystem-related fungal studies are not uncommon in Europe, where distribution data and mapping of agarics are especially extensive. Knowledge of their mycoflora is substantial, permitting demonstration of a recent, dramatic decline in species diversity and (locally) a shift from dominance of mycorrhizal fungi to dominance of saprophytic fungi (Arnolds, 1991). The mycoflora of much of North America is still scarcely known; there are few complete regional floras for comparative study with the Southwest.

Depictions of biotic communities are often based upon floristic data (Brown, ed., 1982; McLaughlin, 1989). Biomes are considered natural formations arising from responses by plants and animals to a set of climatic factors. Since biomes are presumed to have distinct evolutionary histories based upon these physiological responses, comparisons of biotic provinces for shared fungal species, rare species, and widely distributed species may shed light on evolutionary relationships among fungi. The Chiricahuas are located in the Madrean Province derived from the Madro-Tertiary Geoflora and have several distinct biomes which have developed from warm, moist climates, through Tertiary dry periods and Quaternary glacial and inter-glacial periods. The organization of plant species now found in present biomes is a result of Pleistocene and Holocene climatic shifts in North America, with mesophytic evergreen plants spread across the lower southwest and montane species at higher latitudes, but reaching upper elevations of southwestern mountains. Present day biomes of the Chiricahua Mountains, which presumably reflect several paleocommunities are presently arranged vertically. It may be useful to compare fungal species composition in these vertical biomes to other floristic provinces with affinities: Californian (evergreen sclerophyllous scrub and oak woodlands); Pacific Northwest (cold temperate evergreen forests); Southeast (warm temperate evergreen woodlands).

This study is the first attempt to record the mycoflora of the Chiricahua Mountains and the first in North America to document systematically the distribution of the fungi along biome categories. Recognition and delineation of the fungi is a major taxonomic effort, ideally utilizing the efforts of specialists (both taxonomic and geographic). This study is also unique in the participation of several mycologists from various parts of North America, including Mexico, who are specialists in different taxonomic groups.

METHODS

The study area includes much of the Chiricahua Mountains: west, east and south drainages and the crest area near Rustler Park, and sampling in the drier Chiricahua National Monument. Collections were made in 1989, 1990, and 1991 in August during summer monsoon season which can provide up to 130 mm of rainfall in the upper, cold-temperate, montane conifer forests and up to 104 mm in the lower, warm, temperate, evergreen woods. Occasionally more than one site was visited per day. When sites were very productive, more time was required for processing and note taking; in such cases collecting was not done daily. Each distinct locality (site) was described for vegetation (dominant tree species listed first) and elevation and was numbered. Coordinates for sites were recorded using Universal Transverse Mercator 1000 m grid numbers (rather than latitude and longitude) from a USGS 1:24000 scale map. Collecting was not done on standardized plots.

Collections were generally processed by the individual collector, excepting specimens pertaining to the interest of another specialist present. A data card bearing a unique Chiricahua collection number was filled out either at the collecting site or later, to record locality data, substratum or the presumed symbiont (for mycorrhizal species), and to characterize the plant community or ecotone. Specimens were then photographed, described, and dried on mesh racks over an electric heater set at 43%46' C. Dried collections, arranged by Chiricahua collection numbers, are maintained in herbarium cases at the Natural History Museum of Los Angeles County. Collections split and taken with the investigator for study were also provided with Chiricahua numbers.

CHARACTERIZATION OF HABITATS

Based on species composition and climate, Brown & Lowe (in Brown, ed. 1982) refine Merriam's life zones (Lower Sonoran, Upper Sonoran, Transition, Canadian) to 27 biotic communities for Southwest ecosystems. Of these, fungi were collected from two different series of two major biomes: Madrean Evergreen Woodland Forest and Madrean Montane Conifer Forest. A total of 43 sites were visited, which made up 9 distinct vegetation types, then organized into 4 general habitat types, based upon plant species, degree of cover, altitude, and relative humidity:

(A) JQP (Juniper-Oak-Pine; "Encinal"; 1576-1818 m elev.) - dry, open, gentle slopes with sandy to rocky, bare soil, scant leaf litter. Common plants: *Quercus emoryi, Juniperus deppeana, Pinus discolor, P. leiophylla* var. *chihuahuana, Q. arizonica, Cupressus arizonica.*

(B) QPJ (Oak-Pine-Juniper; Riparian; 1636-1939 m elev.) - a rich community, occasionally at same altitude as **A,** but with more plant cover and leaf litter and higher humidity. Common plants: *Quercus arizonica, Q. hypoleucoides, Q. emoryi, Pinus leiophylla* var. *chihuahuana, Juniperus deppeana, P. engelmannii, Platanus wrightii, Juglans major, P. discolor, Pseudotsuga menziesii, Fraxinus velutina, Populus fremontii, Prunus serotina.*

(C) MDE-Transition (Mixed Deciduous-Evergreen; 1879-2424 m elev.) - transition between oak-pine-juniper and mixed conifer forests; temperatures cooler, humidity higher, slopes steeper, high plant cover reducing evaporation. Common plants: *Quercus hypoleucoides, Q. arizonica, Pseudotsuga menziesii, Pinus engelmannii, P. ponderosa* var. *arizonica, Juniperus deppeana.*

(D) MC (Mixed Conifers; 2485-2758 m elev.) - uppermost zone, ranging from narrow ridges with steep sides to open meadows or grassy fields. Either open mature Ponderosa pine stands or pine and fir filled in with abundant Douglas fir. Precipitation as snow and rain. Cool and moist. Common plants: *Pinus ponderosa* var. *arizonica, Pseudotsuga menziesii, Abies concolor,* occasional *Populus tremuloides.*

RESULTS

A total of 362 species of macrofungi are reported (243 agarics and boletes, 41 aphyllophorales, 28 ascomycetes, 50 others, including gasteromycetes, heterobasidiomycetes, and hypogeous fungi). Replicate collections from the same sampling site are excluded from the analysis, despite their giving some indication of local abundance. Presence or absence only was recorded for a given site since visits to all sites were not equal and sampling was not done on equal size plots. Sites are generally located within at least one UTM-1000 grid area, i.e. at least 1000 m *away* from the nearest other site. Collections from different sites of a given habitat were tallied, because sites were located far enough apart so that the same fungal population is presumably being counted only once. This provides a gauge of frequency and relative abundance.

Only 32 taxa (13.3%) of all agarics and boletes occur in over 10% of sites. Among these commonest species, 72% were mycorrhizal; 28%, saprophytic. Four species occur in 25-33% of all sites. The most widely distributed species (in all habitat types) were *Inocybe rimosa, Suillus wasatchicus,* and *Amanita rubescens sensu auct. amer.*

In general, abundance and species diversity appear to increase with elevation (Table 1). However, distribution by habitat varies greatly. Habitat **B** is rich in oak-pine-juniper species; habitat **D** is rich in conifer species; C is intermediate between them with a mixture of cool temperature oaks and conifers. The anomalous low fungal species number for habitat C cannot be explained at present, given that the number of C habitat collecting sites is nearly equal to that of **D** habitat sites.

Table 1. Relative Species-Richness of Habitats

Habitat	# Sites	Total Taxa	Agarics/Boletes	Ascomycetes	Aphyllo.	Others
A	9	65	44	3	6	12
B	16	161	111	9	14	27
C	8	123	85	13	15	10
D	10	183	132	14	15	22

A majority of fungi collected were not present in all 4 habitats. A preponderance of taxa are limited to one habitat, while a very small number occur in all 4 habitats (Table 2). Interestingly, the same trend is evident for both agarics/boletes (many of which are mycorrhizal) and non-agarics/boletes (some of which are mycorrhizal). This suggests that the diversity of fungal species is not strictly related to fungus-plant mutualisms.

Table 2. Frequency of Occurrence/Habitat

	Agarics/Boletes		Non Agarics/Boletes	
Taxa occurring in 4 habitats	9	3.0%	3	2.5%
Taxa occurring in 3 habitats	26	10.7%	4	3.3%
Taxa occurring in 2 habitats	50	20.5%	25	21.1%
Taxa occurring in 1 habitat	156	65.0%	86	72.8%

The large number of singletons may signify a rarely occurring species or a narrow habitat preference (possibly physiologic range) or pressures of competition. Both agaric/bolete and non agaaric/bolete singletons show a high habitat preference for the conifer zone (D), which has the highest fungal species diversity, but not plant species diversity, **the shortest** growing season, lowest minimum temperature, poor soil (little leaf litter), but compensating somewhat, more dead wood substrates.

Saprophytic fungi are theoretically capable of colonizing all habitats since they will find organic material to decompose in any habitat. It is noteworthy then, that the most diverse, wide-spread, and abundant fungal genera *(Inocybe, Amanita, Boletus,* and *Russula) are* all mycorrhizal and are also the only temperate mycorrhizal genera to occur in the neotropics. In the Chiricahuas, *Inocybe* and *Amanita* have the greatest number of species. They are not only the most widely distributed agarics (worldwide); they also form important components in other North American provinces (Nishida, 1989; Thiers, 1982; Tulloss, pers. comm.). McLaughlin (1986) notes that the greatest overlap of Southwest plr.nt species with peripheral plant provinces is with the Pacific region. Two types of species overlap: species of disturbed or weedy habitats, and species of relatively mesic habitats. *Inocybe* species in the Chiricahuas fit the former category, and their common association with oaks in both regions is important in their distribution.

Amanita and *Boletus* taxa appear to have affinities with fungi of the southeastern United States. Among Ascomycetes, the genus *Helvella* is remarkably represented in the Chiricahuas and distributed in all habitats. Southern and central California have a similarly rich representation of *Helvella* (Menge, pers. comm.).

FUTURE RESEARCH NEEDS

Of the commonest ten genera represented in frequency (number of sites), species diversity, and abundance (number of collections), 80% are mycorrhizal and are widely distributed in the Chiricahuas. Therefore, since they are characteristic of the Chiricahua mycoflora, comparisons with nearby or related local floras may be useful to elucidate historical events such as intense speciation (or extinction), vicariance events, and recent introductions. Complete and accurate determination of Chiricahua species and a substantial study of related regional mycofloras are required for ascertaining affinities. There are presently indications that species with affinities with distantly located species may in fact be distinct and yet undescribed taxa (Tulloss *et al.*, 1992).

Forest decline in Europe appears to be preceded by a drastic decline in fungal production and diversity. Fungi thus may become an indicator of serious problems in the health of forests The signs of serious decline of fungi in European forests suggest an urgent need to establish baseline data in the Chiricahuas and elsewhere, regarding the presence of fungal species and their ecological relationships with other fungi and with plants. At present, the Chiricahuas are blessed with relatively unpolluted air and a generally low disruptive use by people and are perfect for an ongoing investigation of the fungi present in a relatively pristine ecosytem.

ACKNOWLEDGEMENTS

An invitation from the Arizona Plant Society in 1983 prompted in the senior author a keen interest in establishing a study of the mycoflora of the Chiricahua Mountains of SE Arizona and in organizing an on-going, multi-specialist project. The senior author also thanks Time Inc. Magazines for support of field work. We thank Wade Sherbrooke and his staff at the Southwestern Research Station and Gary Harman at the Pine Canyon Camp for their gracious help, and Robert M. Chapman for logistical support.

LITERATURE CITED

Arnolds, E. J. M. 1991. Decline of ectomycorrhizal fungi in Europe. *Agric., Ecosyst. Environm.* 35: 209-244.

Brown, D. E., ed. 1982. Biotic communities of the American Southwest—United States & Mexico. *Desert Plants* 4(1-4). 342 p.

Fogel, R. and J. M. Trappe. 1978. Fungus consumption (mycophagy) by small animals. *Northw. Sci.* 52: 1-31.

and G. Pacioni. 1989. Materials for a hypogeous mycoflora of the Great Basin and adjacent cordilleras of the western United States. *Mem. New York Bot. Gard.* 49: 119-128.

Gilbertson, R. L. 1974. *Fungi that decay ponderosa pine.* Univ. Arizona Press, Tucson. 197 p.

______. 1981. North American wood-rotting fungi that cause brown rots. *Mycotaxon* 12: 372-416.

. 1984. Relationships between insects and wood-rotting basidiomycetes. pp. 130-165. In: Q. Wheeler and M. Blackwell, eds. *Fungus-Insect Relationships.* Columbia Univ. Press, New York.

and L. Ryvarden. 1986-1987. *North American Polypores. vol.* I & II. Fungiflora, Oslo, Norway.

McLaughlin, S. P. 1989. Natural floristic areas of the western United States. *J. Biogeogr.* 16: 239-248.

Nishida, F. 1989. A Key to the species of *Inocybe* in California. *Mycotaxon* 34: 181-196.

States, J. S. 1983. New records of hypogeous Ascomycetes in Arizona. *Mycotaxon* 16: 396-402.

. 1984. New records of false truffles in pine forests of Arizona. *Mycotaxon* 19: 351-367.

. 1990. Mushrooms and truffles of the Southwest. University of Arizona Press, Tucson. 232 p.

Thiers, H. D. 1976. Boletes of the southwestern United States. *Mycotaxon* 3(2): 261-273.

. 1982. The Agaricales of California. 1. Amanitaceae. Mad River Press, Eureka, CA. 53 p.

Tulloss, R. E., C. L. Ovrebo, and R. E. Hailing. 1992. Studies on *Amanita* (Amanitaceae) from Andean Colombia. *Mem. New York Bot. Gard.* 66: 1-46.

CLIMATIC FACTORS AFFECTING THE ARID-HUMID BOUNDARY AND THE DISTRIBUTION OF WOODLAND VEGETATION IN THE SOUTHWEST

PETER G. ROWLANDS
National Park Service Cooperative Park Studies Unit,
POB 5614, Northern Arizona University, Flagstaff, AZ 86011

Introduction

Since Merriam's (1890) classic study in the latter half of the 19th century, the relationships between the distribution of vegetation (i.e. "zones", formation-types, series, associations etc.) and environmental factors has been a subject of intense study in the American Southwest Among the many phenomena that have been observed, a "biogeographic anomaly" (Martin, 1963; Wells and Burger, 1967; Wells, 1979) is particularly intriguing. As one proceeds south along the Rocky Mountains, various plant communities, including the lower limit of trees, ascend to successively higher levels. But in Arizona and New Mexico, the lower limit of most tree growth does not continue to rise with decreasing latitude; it drops (Martin, 1963). The confounding effect of this "anomaly" on the interpretation of quaternary southwestern paleoecological observations was discussed in terms of palynology by Martin (1963) and in terms of fossil packrat middens by Wells and Berger (1967 and Wells (1979). However, other than recognizing that the fall in elevation of woodlands at lower latitudes from the Southern Great Basin and Mojave Deserts through Arizona and New Mexico into Mexico may be related to increasing precipitation, no rational mechanism for explaining this phenomenon is given. Martin (1963) adds that: "in the southwest, any major increase in moisture will depress all montane vegetation zones."

The objective of my research is to (1) explore the changes in the relationships between precipitation, evapotranspiration and elevation along a morthwest to southeast gradient from the northern Mojave and Southwestern Great Basin Desert to southeastern Arizona and (2) suggest a climatic mechanism which may help to explain the decline in the lower limit of forest and woodland with decreasing latitude in the Southwest.

Methods and Data Sources

Data sources for climate included Mallery (1936), US Department of Commerce, Weather Bureau/NOAA summarized climatic data (U.S. Dept. Commerce Weather Bureau, 1952, 1964 and 1956-1990) and Sellers and Hill (1974). The region under examination is more or less encompassed by the southern portion of the Basin and Range Province from the Death Valley area in the northwest to the Tuscon-southeastern Arizona area in the southeast. The region was broken up into three discrete subregions: the northern Mojave-southwestern Great Basin subregion (n=12 weather stations), West-Central Arizona subregion (n=14 stations) and the southeastern Arizona Subregion (n=17 stations for temperature, 18 for precipitation). Potential Evapotranspiration was calculated using the Thornthwaite temperature dependent model (Thornthwaite 1948, Thornthwaite and Mather 1957) and is hereinafter referred to as PotE.

Discussion and Conclusions

Major (1977) defined the elevation where PotE and precipitation were equal to each other as the "arid-humid boundary" (i.e., Pote/Ppt=1). Following Major's (1977) model, the lapse rates for PotE and predicted increase in precipitation with elevation can be used to estimate the elevation of the arid-humid boundary in each of the three subregions (Fig. 1, vertical lines A,B and C).

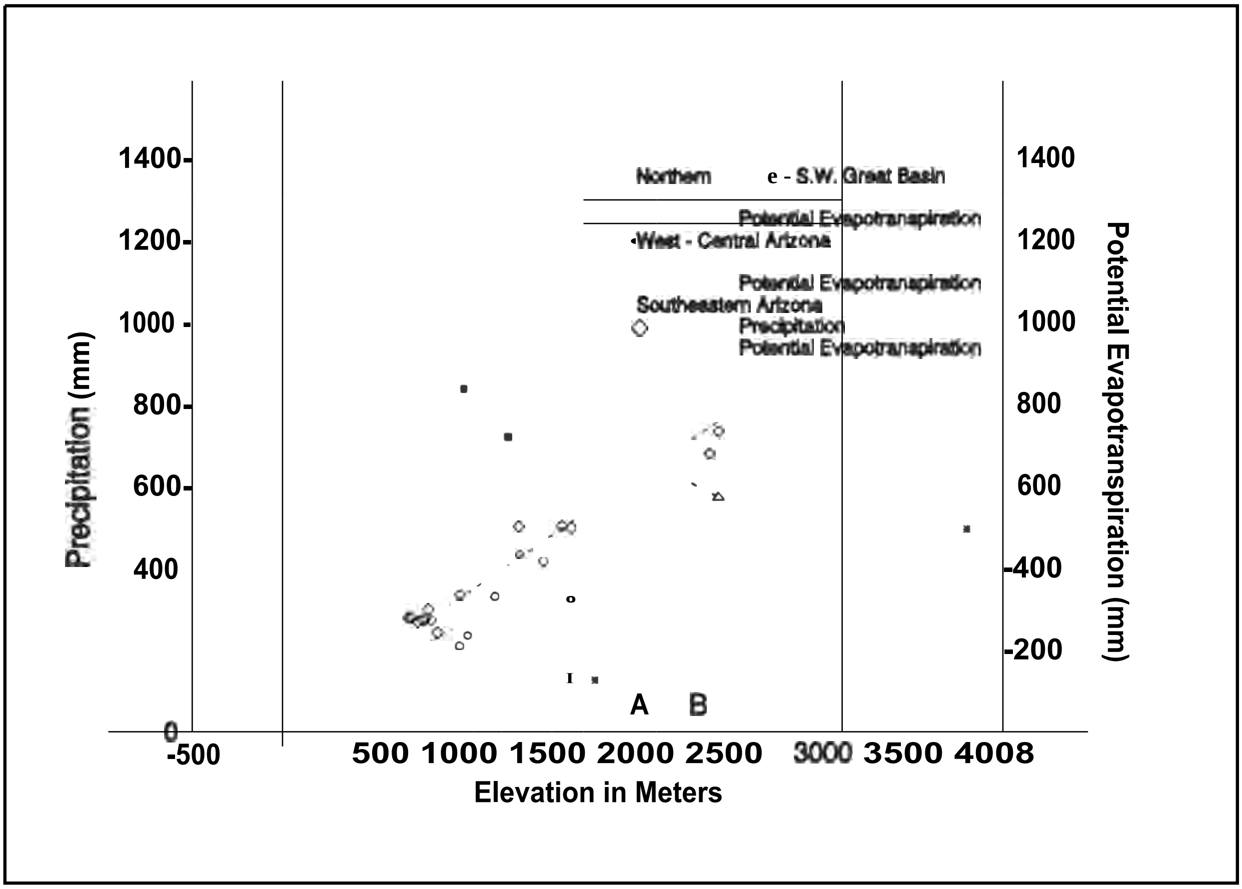


Figure 1. Relationships between the mean annual precipitation and potential evapotranspiration with elevation in the Southwest. All regression lines are significant at $p < 0.01$.

Superimposing the regressions of PotE and precipitation against elevation reveals that the arid-humid boundary declines in elevation by about 900 -1000 m from the northern Mojave-southwestern Great Basin (≈3100 m) to West-Central and southeastern Arizona (ft2100 - 2250 m). Because of the relatively greater warmth at all corresponding elevations throughout the year in southeastern Arizona, the PotE lapse curve is elevated above that of west-central Arizona. As a result, the deflection downward of the arid-humid boundary from west-central Arizona to southeastern Arizona is not as substantive.

Wells and Berger (1%7) and Wells (1978) determined that the relationship between the lower elevational limits of woodlands and degrees north latitude is a 283 meter decline per degree latitude. This is similar, within an order of magnitude, to the approximately 200 meter depression per degree latitude of the arid humid boundary between the northern Mojave-southwestern Great Basin subregion (37°N) and the southeastern Arizona subregion (≈32°N) described above. Wells and Berger (1967) explained that some variance is undoubtedly due to the east-west gradient of decreasing summer precipitation and to local effects of substrate and physiognomy, especially distance from orographic barriers (i.e., rainshadow effects). I conclude that the effect of longitude could be just as important as latitude. The elevation of the arid-humid boundary, and by implication the elevational distribution of forest and woodland, is determined by differences in rates of increase of precipitation with elevation between the subregions; differences mediated by summer rainfall (low to almost nonexistent in the northern Mojave-southwestern Great Basin) which increases primarily as a function of longitude. In support, Wells (197S) asserts that: "the major axis of the latitudinal zonational anomaly actually extends from the northwest to the southeast." Obviously, a longitudinal component is entailed.

Additional corroboration can be gleaned from regional floras and plant distributional studies. On Mount Charleston (≈36°15'N), northwest of Las Vegas, Nevada, well developed stands of ponderosa pine Pinus Donderosa do not occur any lower than about 2200 m, according to Clokey (1951) other than in exceptional situations (Excelsior Canyon, elev. 1200 m). In northern and central Arizona (34°-35°N), according to McDougall, ponderosa pine grows: "mostly between 5500 and 8000 ft (1676 - 2438 m). As in the Charleston Range, trees are occasionally found lower (down to 1070 m) in exceptional situations

The lower elevational limit of Pine Parkland/Forest (Pinus ponderosa) given by Lowe (1961) and Whittaker and Niering (1968) for the Santa Catalina Mountains (Ps32°25'N) is about 2000± m on south slopes and slightly lower on north slopes (1750± m); not substantively different from the lowest elevations cited by McDougall for northern and central Arizona. However, between the Charleston Range and central arizona, the drop in elevation of ponderosa pine forest/parkland is about 500 meters over 2° of latitude or about 250 m per degree; an amount very close to Wells' value of 283 meters per degree.

Literature Cited

CLOKEY, I. W. 1951. Flora of the Charleston Mountains, Clark Co., Nevada. University of California Press, Berkeley.

LOWE, C. H., Jr. 1961. Biotic communities in the Sub-Mogollon Region of the inland Southwest. Journal of Arizona Academy of Sciences 2:40-49.

MCDOUGALL, W. B. 1973. Seed plants of northern Arizona. Museum of Northern Arizona, Flagstaff, Arizona.

MAJOR, J. 1977. California vegetation in relation to climate. Pp. 11-74 in The terrestrial vegetation of California (M. G. Barbour, M. G. and J. Major eds.). John Wiley and Sons, New York.

MALLERY, T. D. 1936. Rainfall records for the Sonoran Desert. Ecology 17:110-121.

MARTIN, P. S. 1963. The last 10,000 years, a fossil pollen record of the American Southwest. University of Arizona Press, Tucson.

MERRIAM, C.H. 1890. Results of a biological survey of the San Francisco Mountain region and desert of the Little Colorado in Arizona. North American Fauna 3:1-136.

SELLERS, W. D. and R. H. HILL. 1974. Arizona climate, 1931-1972. University of Arizona Press, Tucson.

THORNTHWAITE, C. W. 1948. An approach toward a rational classification of climate. Geographical Review 38:55-94.

THORNTHWAITE, C. W. and J. R. MATHER. 1957. Instructions and tables for computing potential evapotranspiration and water balance. Drexel Institute Technical Publications in Climatology 10:183-311.

U. S. DEPT. OF COMMERCE, WEATHER BUREAU. 1952. Climatic Summary of the United States: Supplement for 1931-1952. U. S. Government Printing Office.

U. S. DEPT. OF COMMERCE, WEATHER BUREAU. 1964. Climatog.aphy of the United States No. 86. Decennial Census of United States Climate—Climatic Summary of the United States, Supplement for 1951-1960. U. S. Government Printing Office.

U.S. Dept. of Commerce, Weather Bureau (National Atmospheric and Oceanographic Administration). 1956-1990. Climatological data for California, annual summaries. U. S. Government Printing Office.

WHITTAKER, R. H. and W. A. NIERING. 1968. Vegetation of the Santa Catalina Mountains, Arizona III Species distribution and floristic relations on the north slope. Journal of the Arizona Academy of Sciences 5:3-21.

WELLS, P. V. 1979. An equable glacio-pluvial in the West: Evidence of increased precipitation on a gradient from the Great Basin to the Sonoran and Chihuahuan Deserts. Quaternary Research 12:311-325.

WELLS, P. V. and R. BERGER. 1967. Late pleistocene history of coniferous woodland in the Mojave Desert. Science 155:1640-1647.

DISTRIBUTION OF MUSHROOMS, MYCOPHAGISTS AND CONIFERS ON SKY ISLANDS OF THE SOUTHWEST

Jack S. States
Department of Biology, Northern Arizona University
Flagstaff, AZ 86011

Introduction

The vast stands of conifer forests on sky islands in the American Southwest are virtually unexplored for many groups of decomposer fungi, particularly the mycorrhizal hypogeous fungi, truffles and false truffles. These fungi have been recognized in recent years as important ectomycorrhizal symbionts whose capacity to accumulate mineral nutrients and water is highly consequential in studies of nutrient cycling and regeneration in forest ecosystems (Fogel and Hunt 1983, Vogt et al.1981).

Over the past ten years I have been collecting materials for a mycoflora of the Southwest (States 1983,1984,1990). An unexpected diversity and abundance of mycorrhizal fungi was found in association with pine forests. Many of the truffles encountered were new or unreported for this region. Furthermore, an interesting tree-truffle-squirrel interaction was discovered. An analysis of this interactive dependency may provide an explanation of the present distribution patterns of the several subspecies found within all three groups and produce evidence regarding their evolutionary history.

Details of the tripartite interaction determined thus far indicate potential co-evolutionary relationships where:

1. Epigeous and Hypogeous fungi form obligate, mutualistic associations with conifers and derive their nutrition from the root systems of the tree mycorrhizae.

2. As a benefit of a mycorrhizal association, water and mineral uptake is enhanced through the increased surface area of absorbtive mycorrhizal roots.

3. Hypogeous, mycorrhizal fungi are dependent on mycophagists (mycovores), primarily rodents, for dispersal of reproductive units (fruiting bodies and spores) since these are produced underground. The highly nutritious tissue of truffles is a major component in the diet of tree squirrels.

4. Viability of reproductive units during passage through the squirrel gastro-intestinal tract and defecation on the forest floor establishes an inoculum potential in the soil for recolonization of conifer roots and mycorrhizal development in seedlings.

5. Species-specific, obligatory relationships have developed between tree host and mycorrhizas:Pinus ponderosa - Rhizopogon ochraceorubens; Pinus edulis - Rhizopogon pinyonensis; Pseudotsuga menziesii- Rhizopogon vinicolor.

The present distribution of the tassel-eared tree squirrel, Sciurus aberti, is coincident with forests dominated by ponderosa pine, Pinus ponderosa, in the southern Rocky Mountains and the Cordilleras of Arizona, New Mexico, and northern Mexico. The genetic uniqueness of the five recognized subspecies and the restriction of their populations to the geographical limits of ponderosa pine (Wettstein and States 1986, Wettstein et al. 1990) suggests co-evolutionary dependence. This association exists only with the Rocky Mountain races of ponderosa pine which have been biochemically differentiated on the basis of xylem monoterpenes and isozyme differences (Conkle and Critchfield 1988). Selective herbivory on inner bark by S. aberti aberti in Arizona was found to be correlated with terpene composition and concentration (Zhang and States 1991). Selection of "feed" trees in Colorado by S. aberti ferreus was also related to terpene composition, but a distinctly different combination of terpene present suggests a unique association in the two geographical regions.

Paleoclimatic changes in the Southwest during the Pleistocene and early Holocene have been used to interpret changes in the flora and fauna (Axelrod 1986). Ponderosa pine has a relatively uncharted history but it clearly responded to the widely fluctuating environment during full glacial and interglacial episodes. It can be reasonably assumed that ectomycorrhizal fungi made adaptive responses to adaptive radiation of the host. Hypogeous fungi are diverse and abundant as pine associates (States 1984,1985). Part of the response to the pine environment has been hypothesized to be a change from an epigeous habit to a hypogeous position. By so doing, water loss was reduced, frost protection was provided, and mycophagists became necessary for spore dispersal.(Bruns et al. 1989).

Conclusions

Investigation of modern geographic distribution of the tassel-eared squirrel: ponderosa pine: mycorrhizal truffle association on the sky-islands of the Southwest can provide clues to the evolutionary history of the associates themselves. A study of the ecological biogeography and evolutionary biology of the interaction is continuing under three major objectives:

1. Coevolution of hypogeous fungi and conifer associates as represented by microspeciation of mycorrhizal fungi in response to host differences and changes.

2. Mycorrhizal dispersal patterns by mycophagists providing a system for testing dispersal rate of fungi compared to that of hosts.

3. Analysis of modern biogeographic distribution to recognize avenues and barriers to co-dispersal into new habitats and the identification of adaptive shifts to changing habitats.

Literature Cited

Axelrod, D. I. 1986. Cenozoic history of some western American pines. Ann. Missouri Bot. Gard. 73:565-641.

Bruns, T.D., R. Fogel, T.J. White, and J.D. Palmer. 1989. Accelerated evolution of a false-truffle from a mushroom ancestor. Nature 339:140-142.

Conkle M. T., and W. B. Critchfield. 1988. Genetic variation and hybridization of ponderosa pine. Pages 27-43 in D. M. Baumgartner and J. E. Lotan, editors. Ponderosa pine, the species and its management. Cooperative Extension,Washington State University, Pullman.

Fogel, R., and G.A. Hunt. 1979. Fungal and arboreal biomass in a western Oregon douglas-fir system: Distribution patterns and turnover. Canad. J. For. Res. 9:245-256.

States, J. S. 1983. New records of hypogeous ascomycetes in Arizona. Mycotaxon 13:396-402

States, J. S. 1984. New records of false truffles in pine forests of Arizona. Mycotaxon 14: 351-367.

States, J. S. 1985. Hypogeous, mycorrhizal fungi associated with ponderosa pine: sporocarp phenology. Page 271 in R. Molina, editor. Proceedings of the 6th North American conference on mycorrhizae. Forest Res. Lab., Oregon State University, Corvallis.

States, J. S. 1990. Mushrooms and truffles of the Southwest. University of Arizona Press, Tucson.

Vogt, K. A., R. L. Edmonds, and C. C. Grier. 1981. Biomass and nutrient concentrations of sporocarps produced by mycorrhizal and decomposer fungi in Abies amabilis stands. Oecologia 50: 170-175.

Wettstein, P. W. and J. S. States. 1986. The major histocompatibility complex of tassel-eared squirrels. II. Genetic diversity asssociated with Abert squirrels. Immunogenetics 24:242-253.

Wettstein, P. W., R. Chakraborty, J. States, and G. Ferrari. T-Cell receptor genes in tassel-eared squirrels (Sciurus aberti). I. Genetic polymorphism Immunogenetics 32:219-230.

Zhang, X., and J. S. States. 1991. Selective herbivory of ponderosa pine by Abert squirrels: a re-examination of the role of terpenes. Biochemical Systematics and Ecol. 19:111-115.

FIRE AND FLOOD HISTORY IN RHYOLITE CANYON, CHIRICAHUA NATIONAL MONUMENT

Thomas W. Swetnam, Christopher H. Baisan, Anthony C. Caprio, and Peter M. Brown
Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ 85721

Introduction

Wildfires burned frequently in the forests, woodlands and savannas of southern Arizona before the turn of the last century. The ubiquity of fire on the pre-1900 landscape is attested to by tree-ring evidence that we have compiled from many desert island mountains of this region (Swetnam 1983, Dieterich 1983, Swetnam et al. 1989, Swetnam 1990, Baisan and Swetnam 1990, Grissino-Mayer 1991, Ortloff 1991, Baisan 1991). Low intensity fires swept wave-like through the understory of conifer forests once or twice per decade for centuries before livestock grazing and fire suppression ended this ancient pattern.

Fire scars formed on the lower boles of resinous pine trees have been the primary source of evidence for the episodic fire patterns. These records can be very detailed and informative. We have sampled and analyzed hundreds of fire-scarred trees with 10 to 20 fire events per tree recorded over periods of more than three centuries. Not only can we determine past fire dates to the year, but in most cases we can also estimate the season of the fires by observing the relative position of the fire scars within the annual rings. Based on these observations, it is evident that the most common season of fire occurrence in southern Arizona in pre-Anglo settlement times (approximately pre-1880s) was in the late spring to mid-summer.

Results and Discussion

We reconstructed a detailed chronology of fire occurrence from Rhyolite Canyon, Chiricahua National Monument by sampling fire-scarred trees throughout the length of the canyon, as well as in the upland reaches of Totem Canyon (a small tributary to Rhyolite) and an adjacent saddle between Rhyolite and Jesse James Canyon. We also collected a few specimens from Surprise Canyon, which is located just north of Rhyolite Canyon. Our initial work (Swetnam et al. 1989) showed that before 1801 fires were widespread throughout Rhyolite Canyon. An unusual 50-year "gap" (1801-1851) with no fires was documented for the upper portion of the canyon above the confluence with Sarah Deming Canyon. Such an extended fire-free period embedded within a more than three-century episodic fire record was unprecedented among more than 30 fire histories we have reconstructed for the southwestern U. S. In the two centuries prior to the gap the mean length of fire-free intervals was 11 years, and fire-free intervals varied in length between 3 and 19 years. Although widespread fires ceased to burn in the upper portions of the canyon during the gap, fires continued to be recorded by our sample trees in the lower canyon.

We hypothesized that the 50-year interruption in the fire regime was due to a debris flow or flood event that scoured the canyon bottom, or otherwise created a fire barrier in the mid-portion of the canyon, and this barrier prevented fires from sweeping up the canyon from the lower elevations. Terraces originating form old debris flows of unknown age are visible at many locations along the canyon bottom. A "debris flow" is effectively a flood of soil, rocks, and water that moves quickly down a slope or watercourse, and eventually is deposited in a layer when the velocity slows to the point where the heavy materials settle out. Debris flows are a common phenomena in semi-arid environments where rainfall is infrequent, but often intense when it does come. Debris flows have been linked to fire events (e.g., southern California chaparral fires) because some fires denude the ground, encouraging fast runoff over soils no longer held in place by vegetation. A key condition for such an event may be a short interval between the fire and the rainfall event, i.e., before grasses or other plants can resprout or re-establish and help stabilize the soil.

Following our initial work we attempted to test our hypothesis that flood or debris flow events were responsible for the 50-year gap observed in the Rhyolite fire chronology. Our strategy was to obtain tree-ring samples from (1) trees growing along the bed of Rhyolite that were scarred by past flood events, (2) from trees that were growing on the debris flow terraces at the mouth of Sarah Deming, and another terrace in lower Rhyolite Canyon, and (3) from additional fire scarred trees in the uplands.

The methods of sampling flood-scarred trees to reconstruct flood history was recently documented and demonstrated by Dr. V. A. S. McCord (1990). This approach relies on tree-ring sampling and dating of injuries caused by floods or debris flows to surviving trees along the path of the flood or debris flow. These injuries can usually be distinguished by their appearance from other causes of injury, such as fire. Our sampling of trees growing on the terraces was aimed at determining a minimum age of the terrace. Ages of these trees (determined by taking increment cores at the base of the trees) would give us an estimate of the time of their establishment, which would necessarily occur sometime (years to decades) after the terrace was formed. Sampling of additional fire-scarred trees in the uplands was directed at determining if the 50-year gap was also present in the higher elevation areas above the rim of the canyon. If it was, then this would suggest that fires prior to the gap were spreading from lower elevations, and were somehow prevented from spreading to the uplands during the gap. If no gap were present in the fire records from the uplands, then the gap would be identified as specific to the canyon itself, and a sufficient source of fires was present in the uplands, or there was another route from the lowlands, to maintain episodic fires without long intervals (i.e., 50 years).

A summary of the results are as follows:

1. Five flood dates were determined from increment borings of flood-scarred trees in Rhyolite or Sarah Deming: 1866, 1881, 1888, 1937, and 1954.
2. Approximate establishment dates of 13 pine trees growing on the terrace at the mouth of Sarah Deming were clustered in the period 1870-1900 (11 trees), with one tree establishing much earlier, at about 1825, and one tree establishing later at about 1915.
3. Approximate establishment dates of 10 pine trees in lower Rhyolite was in the 1870s (2 trees), 1890-1920 (7 trees), and one establishing earlier at about 1845.
4. The upland area fire scar samples recorded a single fire during the period 1801-1851. Thus, while the 50-year fire interval was not present here, a 31-year gap was.

We did not identify any flood dates in the early 1800s that might explain the 50-year fire gap. However, we strongly suspect this was because evidence of older floods is relatively rare and thus harder to find. Most trees scarred by earlier floods (before mid-1800s) probably have died, burned up, or decayed. Also, earlier flood scars on living trees tend to be healed over and are not visible (McCord 1990). We identified a number of old snags with flood scars, but we could not effectively take increment cores from these trees (because of decay), and partial sectioning or felling was not permitted. The 1866 flood date does not appear to have affected the fire regime, since fires were recorded later in this decade within the canyon.

The approximate establishment dates of the trees on the Sarah Deming or lower canyon terrace are also later than the hypothesized early 19th century flood/debris flow event. However, it is possible the 1870s-1900 establishment period for these trees was related to the 1866 or 1881 flood events. At this point these are speculative conclusions as we do not currently know enough about the establishment patterns of conifers on debris flow terraces, especially with regard to the possible lag time between formation of a terrace and successful tree establishment.

Although the possible influence of floods or debris flows on fire regimes in Rhyolite Canyon remains undetermined, the fire scar evidence from the uplands does indicate that fires in this area were associated with fire occurrence in the canyon. The upland trees generally recorded the same fire dates as recorded throughout the canyon during the period before the gap. After the gap fire dates in the uplands were different from fire dates in the lower canyon, but they were synchronous with fire dates in the upper canyon (above Sarah Deming). The gap in the uplands is shorter than the gap in the upper portion of the canyon, but it was still the longest fire-free period in the three centuries before 1900. We infer from these patterns that pre-1801 fire occurrence in the uplands areas was at least partially dependent upon fire spread from the lowlands up through the canyon. Apparently, the canyon was eliminated as a major spreading route of fire after 1801. The precise reason for this is not yet known, but we suspect that floods or debris flows may have been involved.

We have not been able to discover flood or debris flow evidence that would help us explain the 50-year fire gap in terms of flood or debris flow dynamics. It is possible that this hypothesis is incorrect. Other explanations include (1) climate variations, and (2) human-related impacts. The 1830s to 1840s was one of the wettest periods in the southwest during the past three or more centuries (Fritts 1991), thus, reduced fire occurrence in a portion of the 50-year gap may be related to a climate-related reduction in fire occurrence and spread. Grazing of livestock may have increased in the lower elevation areas of the Chiricahuas in the 1820s when a truce with the Apaches was in effect for a while and an expansion of Mexican ranchos took place (Swetnam et al. 1989, Bahre 1991). We have observed that the final end of episodic fire regimes in the late 1800s in many locations of the western U. S., including at Rhyolite Canyon, coincides closely with the beginning of intensive livestock grazing, when the fine grassy fuels necessary for fire spread were reduced.

Conclusions

Although this study has failed to conclusively determine the cause of the 50-year fire gap, it has demonstrated the complexity of spatial and temporal disturbance patterns on the landscape of Rhyolite Canyon area of Chiricahua National Monument. It is obvious from abundant visible evidence in the canyon that flood and debris flow events have been major disturbance factors in this canyon in the past. It is reasonable to infer that there has been some interaction of the fire, flood and debris flow regimes. The complexity of the interactions of these disturbances and climate is a source of great wonder and scientific curiosity on our part. On the one hand we are somewhat frustrated in not immediately unlocking the secrets of the complexity we see, but on the other hand we are pleased that the puzzle continues. We plan to expand our work in the Chiricahuas, and other mountain ranges in Southern Arizona and northern Mexico, to the investigation of disturbance patterns in other canyon systems. As this work progresses we believe that we will be able to enrich the understanding and interpretation of the natural history of this region.

Literature Cited

Bahre, C. J. 1991. A Legacy of Change: Historic Human Impact on Vegetation of the Arizona Borderlands. The University of Arizona Press, Tucson. 231 pp.

Baisan, C. H. 1991. Fire scar dates for the Catalina Mountains, Arizona. Unpublished report on file Laboratory of Tree-Ring Research, University of Arizona, Tucson.

Baisan, C. H. and T. W. Swetnam. 1990. Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, U.S.A. Canadian Journal of Forest Research 20:1559- 1569.

Dieterich, J. H. 1983. Historia de los incendios forestales en la Sierra de los Ajos, Sonora. Centro de Investigaciones Forestales del Norte, Instituto Nacional de Investigaciones Forestales, Nota Technica No. 8.

Fritts, H. C. 1991. Reconstructing Large-Scale Climatic Patterns from Tree-Ring Data. University of Arizona Press. 286pp.

Grissino-Mayer, H. 1991. The recent fire history of Mt. Graham and its relevance to an endangered subspecies of red squirrel. Annual Meetings of Pacific Coast Geographers, 11-14 September, 1991, Tucson, Arizona.

McCord, V. A. S. 1990. Augmenting flood frequency estimates from flood-scarred trees. PhD dissertation, University of Arizona, Tucson, AZ. 182.

Ortloff, W. 1991. Fire scar dates for the Santa Rita Mountains, Arizona. Unpublished report on file at Laboratory of Tree-Ring Research University of Arizona, Tucson.

Swetnam, T. W. 1983. Fire scar dates for Sierra Ajos, Sonora, Mexico. Report prepared for USFS, Rocky Mountain Forest and Range Experiment Station, Tempe, Arizona. Unpublished report, on file at Laboratory of Tree-Ring Research, University of Arizona, 10 pp.

Swetnam, T. W. 1990. Fire history and climate in the Southwestern United States. In: Krammes, J. S., tech coord. Proceedings of the Symposium on Effects of Fire in Management of Southwestern Natural Resources, 15-17 November 1988, Tucson, Arizona. USDA Forest Service, General Technical Report RM-191:6-17.

Swetnam, T. W., C. H. Baisan, P. M. Brown, and A. C. Caprio. 1989. Fire history of Rhyolite Canyon, Chiricahua National Monument. Cooperative National Park Service Resources Studies Unit, University of Arizona, Tucson, Technical Report No. 32. 47pp.

MANAGEMENT OF A RARE LILY, *LILIUM PARRYI,* AT RAMSEY CANYON PRESERVE

Tom Wood, Preserve Manager
The Nature Conservancy
Ramsey Canyon Preserve
27 Ramsey Canyon Road
Hereford, AZ 85615

Introduction

The Lemon Lily, *Lilium parryi* Watson, is the only member of the genus *Lilium* which occurs in Arizona. The species was given category 2 status by the U.S. Fish and Wildlife Service in 1980. Fewer than 25 populations with less than 3500 plants (Newman 1990)are known to occur in four disjunct mountain ranges: the Huachuca and Santa Rita Mountains in southeastern Arizona and the San Gabriel and San Jacinto Mountains in southern California. A large, showy perennial, the Lemon Lily is limited to habitats with rich, wet soils at elevations above 1670 m (Toolin 1982). All locations in Arizona are either streamside or in association with springs or seeps.

The Nature Conservancy's Ramsey Canyon Preserve is a 300-acre preserve along a perennial stream in the Huachuca mountains. The preserve provides habitat for a number of rare species including the Lemon Lily. Monitoring of lily populations began in 1980 when 83 plants were found, but by 1987 the preserve population had declined to only 28 plants. Even more alarmingly, the reproductive success of the population appeared to be declining at a rate even greater than the decline in the number of individuals (Warren 1989). A management meeting involving representatives of The Nature Conservancy, the U.S. Forest Service, the U.S. Fish and Wildlife Service, and Arizona Game and Fish was held to determine management options and contingencies. The first issue to be addressed before any meaningful recovery plan could be considered was the reason for the population decline in Ramsey Canyon. If it were found to be a natural decline, not a result of human activity, then intervention would not be appropriate. If, on the other hand, the decline was an artificial situation, then management to reverse the decline was called for.

Upon examination it was clear that, although the factors affecting the lilies were complex, the main cause of the decline was the downcutting of Ramsey Creek following the 1983 flood. Lilies in Miller Canyon, 10 km away, seemed unaffected by the same storm. The difference in the two canyons, drastically affecting the severity of flooding, was a wildfire which occurred in Pat Scott Canyon, a side canyon in the Ramsey Creek watershed, in June of 1983. This fire completely denuded a large area of

Pat Scott Canyon and, combined with an exceptionally heavy rainfall, produced record flooding in Ramsey Canyon. The stream became entrenched and downcut over a meter in places. The local water table in the wet soil pockets was lowered, drying the soil below the soil moisture threshold needed by the lilies. When compared with the sites at which the lily is found elsewhere in the Huachucas, Ramsey canyon sites now appear distinctly drier than the other three canyons (Warren 1989). Fire is a natural part of the mountain ecosystem, but the severity of the fire was the result of elevated fuel loads, an artifact of fire management practices. The natural fire regime in the region calls for a low intensity fire every 8-10 years to sweep though an area, reducing fuel loads, opening up the canopy, and stimulating fire dependent plants. The Pat Scott Canyon area had not been allowed to burn for over 40 years. Thus fire management practices could be directly related to the lily's problems in Ramsey Canyon.

Once we decided action was justified, the next question was what action to take. Should we transplant lilies from a healthy population elsewhere to Ramsey? This seemed inadvisable until the genetic variability between populations was ascertained. Should we plant lilies in what we deemed suitable habitat? This stop-gap measure until a fire management plan to protect the watershed can be adopted seemed justified. After the agreement to plant seeds collected in Ramsey, we were disturbed to find only two flowers blooming, one on the preserve and one in the National Forest. Unsure that the normal pollinator, a hawk moth, (Skinner 1988) would find both flowers, we artificially pollinated the two flowers in Ramsey. Six weeks later we collected 300 seeds from the two plants. One hundred seeds were stored in a seed bank to provide a second chance if needed. One hundred seeds were planted near the parent plants and the remaining one hundred seeds were planted along the new stream level in shaded moist habitats. Germination rate the first year was 28%. Seeds were again collected from the two 1990 flowers and planted in appropriate habitat. By May of 1991 a high census of 94 plants (16 adults, 35 second-year plants, 43 seedlings) were found. In addition, the population in the National Forest produced 101 plants and 16 flowers. How much of the recovery is due to time and a good, wet spring is hard to quantify, but it seems likely that some of the "new" populations will become established. Much remains to be done before we can assume that the lily is secure in Ramsey Canyon.

A comparison of the genetic variability within and among the Arizona and California populations was conducted by Yan Linhart, University of Colorado. He found that the California populations showed greater genetic variability than their Arizona counterparts. In Arizona, the least variable population was numerically the largest and the smallest population was among the most variable. These findings underscore the need for a genetic perspective in conservation matters (Linhart and Premoli 1992).

Future research and management needs

Future research and management needs for the Lemon Lily are multi-leveled. On the organism level we need a better understanding of the life history and ecology of the Lemon Lily. It has been assumed, based on other lilies, that the Lemon Lily is essentially self-sterile (Newman 1990). The high degree of inbreeding found in the genetic research and the isolated nature of the populations suggest that this may not be true in Lemon Lilies; more research is needed. A better understanding of the habitat requirements and continued careful monitoring of the seedling and adult plants is needed for management of existing populations.

On the ecosystem level, a greater understanding and appreciation for watershed management and the impact of fire management practices on riparian habitats and species is needed to insure the survival of the Lemon Lily in these mountain canyons.

Literature cited

Linhart, Y.B. and A. Premoli. 1992. Genetic erosion in *Lilium parryi*. Unpublished.

Newman, D. 1990. Element Stewardship Abstract - *Lilium parryi*. The Nature Conservancy, Tucson, Arizona.

Skinner, M.W. 1988. Comparative pollination ecology and floral evolution in Pacific Coast *Lilium*. Harvard University dissertation, Cambridge, Massachusetts.

Toolin, L.J. 1982. Status report: *Lilium parryi*. Office of Endangered Species, U.S. Fish and Wildlife Service, Albuquerque, New Mexico.

Warren, P.L., L.S. Anderson, and P.B. Shafroth. 1989. Population studies of Sensitive plants of the Huachuca and Patagonia Mountains, Arizona. The Nature Conservancy, Tucson, Arizona.

THE ECOLOGY OF ANIMALS
IN THE CHIRICAHUA MIOUNTAINS

HABITAT ASSOCIATIONS OF BIRDS AND HERPETOFAUNA IN SOUTHEASTERN ARIZONA

William M. Block and Kieth E. Severson
U.S.D.A. Forest Service, Rocky Mountain Forest and Range
Experiment Station, Forestry Sciences Laboratory, ASU,
Tempe, AZ 85287-1304

Introduction

The mountains of southeastern Arizona support a large diversity of vegetative plant communities ranging from grassland and desert scrub to spruce-fir forests. These vegetation types provide appropriate conditions for a number of species of vertebrates. Although vertebrates have been the subject of numerous studies in this region, most studies were restricted to one species, one mountain range, or one season. This limited scale of observation precludes generalizations of habitat associations between species and their environments.

In 1991, we initiated a research project to evaluate habitat associations of birds and herpetofauna on the insular mountains of southeastern Arizona. This project is scheduled to continue through 1995. Our overall goal is to inventory three classes of vertebrates and their habitats, and to establish a sampling system to be used as a template for a long-term monitoring program to assess the effects of natural and anthropogenic impacts on vertebrate populations.

Specific objectives of the research are to: (1) determine distributions and abundances of birds; (2) evaluate macro- and microhabitat associations of birds; (3) determine patterns of resource use by a subset of neotropical migrant birds; (4) determine distributions and abundances of reptiles and amphibians inhabiting riparian environments; and (5) describe microhabitats of reptiles and amphibians in riparian areas.

We are using the point-count method to sample bird abundances; 250 counting stations have been established among the mountain ranges. Additional stations will be established in 1992. Counting stations sample oak *(Quercus* spp.), oak-juniper *(Juniperus* spp.), pine *(Pinus* spp.)-juniper, and pine-oak woodlands, and mixed-conifer forests. Observers record all birds detected within a fixed 5-min period at each station. Points are sampled three times each season to account for temporal variations in bird detectabilities.

Physiognomic and vegetative variables are measured within four 0.1-ha circular plots to characterize the habitat. Bird numbers will be correlated to these habitat variables to assess detailed habitat associations.

We are collecting data pertaining to foraging and nest sites of warblers and tanagers to assess aspects of resource use on a finer scale. These data will detail species, size, shape, and vigor of specific trees and substrates used for foraging and nesting.

Time-constraint sampling is being used to assess the distribution and abundance of reptile and amphibian populations. All sampling is being done in riparian habitats and along drainages. This method entails two people searching on, under, and in all possible substrates where an amphibian or reptile might be found for a fixed period of 4 person-hours. Once an animal is located, search time is temporarily suspended while the animal is captured, measured, and released, and information is recorded pertaining to the habitat within a 2.5-m radius of where the animal was found.

Our results are preliminary, representing data from the first year of a study that is scheduled to last five years. We feel that five years is the minimum duration needed to incorporate temporal variations in abundances, distributions, and habitat use. Failure to account for such environmental variations may result in incomplete or misleading information.

Conclusions and further research

Observers detected 117 avian species during point counts. Of these species, 78 were detected on the Chiricahuas, 69 on the Huachucas, 52 on the Pinalenos, 71 on the Santa Catalinas, and 76 on the Santa Ritas. Counting stations on the Pinalenos were restricted to one vegetation type (oak-juniper woodland), which accounts for the relatively low number of species detected there; multiple vegetation types were sampled on the other mountain ranges. We will enlarge our sampling efforts to include more vegetation types on the Pinalenos in 1992.

The species detected across all mountain ranges included 59 resident species that occur year-round and 58 species of neotropical migrant birds, most of which breed in these mountains but winter in tropical environments of Mexico and Central and South America. Neotropical migrant birds are of particular concern because of recent evidence that suggests precipitous population declines of some species throughout North America.

Observers conducted a total of 48 time-constraint searches on the Chiricahua, Huachuca, Santa Rita, and Santa Catalina mountains during July, August, and September 1991. They captured 444 individuals representing 23 species of herpetofanua, with 10 to 13 species represented on each mountain range. Lizards were captured more frequently than any other taxon, with *Sceloporus jarrovii* being captured most frequently. Other lizards sampled included: *S. clarkii, S. scalaris, S. virgatus, S. undulatus,* ***Holbrookia*** *maculata, Urosuarus ornatus, Elgaria kingii, Phrynosoma douglassi, Cnemidophorus sonorae,* and *C. exsanguis.* Seven species of snakes were sampled: *Lampropeltis pyromelana, Masticophis bilineatus, Thamnophis cyrtopsis, Crotalus lepidus, C. molussus, C. viridis,* and *C. willardii.* Five amphibians were captured: *Ambystoma tigrinum, Bufo punctatus, Hyla areniclor, H. eximia,* and *Rana castebeiana.*

These results provide only a cursory example of the types of information we are collecting. Presently, it is premature to expand upon these data or to present specific habitat, foraging, and nest data until the study is completed. When completed, however, this study should provide important information for the management of wildlife in southeastern Arizona.

In a general sense, the data will help to define the biodiversity of the sky islands. Specifically, we will provide information on habitat associations of the birds and herpetofauna that we are studying. Habitat descriptions will range from general associations of these vertebrates with general vegetation types, to detailed descriptions of the habitat components for some species. Data from these detailed descriptions will be used in the development of predictive, quantitative habitat models. These models will be particularly important for assessments of habitat suitability and for predicting the effects of habitat change on these species. Further, our bird counts will provide bird abundance data for five years, and a firm basis for long-term population monitoring.

A PRELIMINARY UNDERSTANDING OF MEXICAN SPOTTED OWL HABITAT AND DISTRIBUTION IN THE CHIRICAHUA MOUNTAINS AND ASSOCIATED SUB-MOGOLLON MOUNTAIN RANGES IN SOUTHEASTERN ARIZONA

Russell B. Duncan and Joshua D. Taiz
Southwestern Field Biologists, Tucson, Arizona

Species Overview

The Mexican spotted owl *(Strix occidentalis lucida)* is one of three recognized spotted owl subspecies (American Ornithologist's Union 1957). It ranges from southern Utah, southern Colorado, south through Arizona and New Mexico, and extreme western Texas, and into the Sierra Madre Occidental, Sierra Madre Oriental, and the Mexican Transvolcanic Range (Sierra de Anáhuac) of Mexico (McDonald et al. 1991).

The distribution of Mexican spotted owls (hereafter referred to as SPOW) is generally patchy and appears to reflect the availability of forested mountain and montane riparian canyon habitats containing uneven-aged, multistoried forests and woodlands with a closed canopy. In Arizona and New Mexico, spotted owls have been found most often from 6,000-9,000 feet elevation in Rocky Mountain montane conifer forests and Madrean evergreen woodlands (Ganey and Balda 1989; Ganey et al. 1988, 1992).

In southeastern Arizona, SPOW nest in all of the major forested mountains including the Chiricahua mountains, Huachuca, Pinaleno, Santa Rita, and the Santa Catalina-Rincon complex (Ganey and Balda 1989). Limited numbers of nesting records have come from smaller, lower elevation ranges, including Atascosa-Pajarito, Galiuro, Whetstone, and Winchester mountains (R.B. Duncan, unpubl. data). In the larger ranges, the mean elevation associated with nesting and roosting SPOW was ca. 2195 m. The highest elevation was ca. 2700 and the lowest elevation was 1645. Depending on aspect, mean elevation habitat usually corresponded to Madrean evergreen woodland or Madrean evergreen woodland/Rocky Mountain montane conifer ecotone.

Recently, the Mexican SPOW subspecies was proposed threatened under the Endangered Species Act by the U.S. Fish and Wildlife Service (Federal Register 56:56344-56355). In addition, it is classified as a sensitive species on all U.S. Forest Service (USFS) lands in Arizona and New Mexico (USFS 1991), and the state of Arizona designates SPOW as threatened (Arizona Game and Fish Department 1988).

Natural History and Status in the Chiricahua Mountains

Various published and unpublished sources have documented the presence of SPOW in the Chiricahua Mountains (Lane 1983; Davis and Russell 1991; Arizona Game and Fish Department, Nongame Data Management System 1990; Coronado National Forest, unpubl. inventory and monitoring data 1990-1992; E.D. Forsman, pers. comm. 1989; J.L. Ganey, pers. comm. 1989, R.C. Taylor, pers. comm. 1990, J.T. Marshall, pers. comm. 1991; W.R. Spofford, pers. comm. 1990; H.A. Snyder, pers. comm. 1992; R.B. Duncan, unpubl. data).

The Chiricahua Mountains of southeastern Arizona represents a diverse assemblage of biotic communities, rising abruptly from subtropical and warm-temperate desert and semi-desert grassland communities, through Madrean evergreen woodland oak and oak-pine associations, to ponderosa pine and mixed conifer Rocky Mountain montane conifer forests, and finally reaching into Rocky Mountain subalpine conifer forest at the highest elevations. In addition to a diverse flora, the Chiricahua Mountains contains an assemblage of diurnal and nocturnal raptors that rivals or exceeds the diversity and density of the National Snake River Birds of Prey Sanctuary in Idaho (H.A. Snyder, pers. comm. 1992).

Based on historical and current data there are at least 19 SPOW territories in the Chiricahua Mountains. The habitat types where spotted owls have been identified in the Chiricahua Mts. are similar in type and frequency of occupancy of other mountain ranges in southeastern Arizona. Dominant vegetation identified by the authors at roost and nest groves in the Chiricahua Mountains includes:

1. Rocky Mountain (Petran) Montane Conifer Forest, Douglas-fir *(Pseudotsuga menziesi)-Mixed* Conifer Association (6 sites),

2. Madrean Evergreen Forest and Woodland, Oak-Pine Series, *Quercus spp.-Pinus* spp. Association (6 sites) and Encinal (oak) Series, *Quercus spp.-Pinus discolor-Juniperus deppeana* Association (2 sites), and

3. Relict Conifer Forest and Woodland, Cypress Series, *Cupressus arizonica* Association (5 sites).

Roost and nest grove habitat at all of the sites was closely associated with steep slopes of canyons and drainageways containing mixed riparian deciduous forest and woodland species intermingled with the aforementioned vegetation types. Riparian vegetation was representative of Rocky Mountain riparian deciduous forest and Interior Southwestern riparian deciduous forest associations. For an excellent discussion of the aforementioned biotic communities, series, and associations, the reader is urged to consult Brown (1982).

The structure of these sites was moderately dense to dense multi-storied canopied forests and woodlands. Preferred nest sites include shaded cliffs, tree hollows, witches brooms, and branch platforms. Elevations of nest and roost groves ranged from 1,615-2,621 meters. To date total overstory cover has not been evaluated for any of the roost/nest groves in the Chiricahua Mts. Ganey and Balda (1990) measured 22 roost sites in northern Arizona and found canopy cover to average 85%. canopy cover at many of the sites in the chiricahua Mts., especially the mixed conifer sites, exhibit a similar trend. In the Madrean evergreen woodland habitat, however, canopy cover was as low as 50%, but was usually greater than 70% (R.B. Duncan, unpubl. data).

SPOW diet in the chiricahua Mts. includes a variety of mammals, birds, reptiles, and arthropods, but they relied on woodrats *(Neotoma* spp.) and white-footed mice *(Peromyscus* spp.) as their main source of food biomass (R.B. Duncan, unpubl. data.; E.R Forsman, pers. comm. 1991). This is in agreement with other SPOW dietary research in northern and southern Arizona (Ganey et al. 1988; Duncan and Sidner 1990).

Although **SPOW** roost and nest in dense vegetation in southeastern Arizona, it is apparent from pellet analysis and direct observation that foraging birds utilize a wide variety of habitats (Duncan and Sidner 1990; **R.B.** Duncan, unpubl. data). These habitats include in addition to the previously mentioned roost/nest grove habitats: oak woodland, oak woodland contact with semidesert grassland, and mixed evergreen sclerophyll associations. In many of these areas the openness of the habitats is striking, unlike much of the published habitat descriptions for the three subspecies of **SPOW**.

Like other diurnal and nocturnal raptors, SPOW is an "r-selected" species that maximizes its energy investment in reproduction under conditions of unpredictable prey availability, potentially high nestling and juvenile mortality, and a relatively short adult lifespan. Suitable roosting and nesting habitat with a multistoried, dense canopy cover, and availability of a rodent prey base are among the factors controlling the distribution of the Mexican spotted owl in the Chiricahua Mts. and elsewhere in its range.

Mexican spotted owls have probably existed in geographically disjunct areas since before the Wisconsinian time (40,000 to 11,000 ybp). Landscape evolution in the southwest has been summarized by Brown (1982). Perhaps no where is habitat fragmentation more apparent than in the Sky Islands of southern Arizona and New Mexico. To what degree geographic isolation reflects genetic isolation is unclear. The presence of Mexican spotted owls on the Sky Island mountain ranges could possibly indicate that genetic isolation is apparently not a significantly limiting factor to the owls. This suggests at least minimal dispersion between mountain ranges (W.B. Heed, Univ. of Arizona, pers. comm. 1991). Even on a small scale (within mountain ranges) habitat is often highly fragmented. Based on observations in southeastern Arizona, fragmentation may not be an influential limiting factor to the species.

The Mexican spotted owl as a species is probably not threatened at present, but clearly inappropriate habitat manipulation by land management agencies has the potential to negatively impact individuals or pairs and perhaps sub-populations throughout its range. Timber harvest could disturb Mexican spotted owl habitat, particularly in parts of its range in northern Arizona and New Mexico, as is the case with habitat associated with some northern spotted owl *(S. o. caurina)* populations (Ganey et al. 1988).

In the chiricahua Mts. and elsewhere in southeastern Arizona spotted owl populations are currently not being impacted by timber harvesting. The biggest concerns for land management agencies in southeastern Arizona, however, are fire management policies (e.g controlled-burn programs) and recreational development.

Literature Cited

Arizona Game and Fish Department 1988. Threatened native wildlife in Arizona. Ariz. Game and Fish Dept. Publ. Phoenix, Ariz. 32 pp.

______ 1990. (Unpubl.) Nongame data management system threatened, endangered, sensitive species, and habitat list for Mexican spotted owls in the Chiricahua Mts., Cochise County. 14 pp.

Brown, D.E. (ed.) 1982. Biotic communities of the American Southwest—United States and Mexico. Desert Plants 4:1-342.

Duncan, R.B. and R. Sidner 1990. Bats in spotted owl pellets in southern Arizona. Great Basin Naturalist 50:197-200.

Ganey, J.L. and R.P. Balda 1989. Distribution and habitat use of Mexican spotted owls in Arizona. Condor 91:355-361.

Ganey, J.L., J.A. Johnson, R.P. Balda, and R.W. Skaggs 1988. Mexican spotted owl. Pages 145-150 in: R.L. Glinski et al., (eds.) Proc. of the Southwest Raptor Manage. Symp. and Workshop. Natl. Wildl. Fed., Washington, D.C.

Ganey, J.L., R.B. Duncan, and W.M. Block 1992. (In Press) Use of oak and associated woodlands by Mexican spotted owls in Arizona. in: Symposium Proceedings of the Ecology and Management of Oak and Associated Woodlands: Perspectives in the Southwestern United States and Northern Mexico. USDA Forest Service, Rocky Mt. For. and Range Exper. Sta. Tech. Rept.

Lane, J.A. 1983. A birder's guide to southeastern Arizona. L and P Press, Denver.

McDonald, C.B., J. Anderson, J.C. Lewis, R. Mesta, A. Ratzlaff, T.J. Tibbitts, and S.O. Williams, III 1991. Mexican spotted owl (S[illegible]) status review. Endangered Species Report 20. U.S. Fish and Wildl. Service, Albuquerque. 85 pp.

U.S. Forest Service 1991. Regional Foresters sensitive species list, Region 3. U.S. Forest Service, Albuquerque.

AMPHIBIANS AND REPTILES OF THE CHIRICAHUA MOUNTAINS, A SKY ISLAND IN THE MADREAN ARCHIPELAGO

Charles H. Lowe
Department of Ecology and Evolutionary Biology
University of Arizona, Tucson, AZ 85721

Richard G. Zweifel
Box 354, Portal, AZ 85632

The Chiricahua Mountains lie in a roughly triangular space in Cochise County in southeastern Arizona--The Chiricahua Mountains Area--delimited by highway 80 on the east, 666 on the west, and 1-10 on the north, with Douglas-Agua Prieta at the southern apex on the Arizona-Sonora border (Fig. 1). Table 1 is a checklist of the 72 amphibian (12) and reptilian (60) taxa known to occur in the Area, which is positioned in the Madrean Archipelago.

This archipelago of high mountain islands--the "sky islands" of Heald (1951)--lies in one of five biogeographic corridors found from Baja California on the Pacific side to Tamaulipas on the Atlantic. The Madrean Archipelago extends south-north between the Sierra Madre Occidental and the Colorado Plateau massif. Today, grassland lowlands wholly or mostly surround the montane islands. But from full glacial to the present time there has been a series of community replacements from forests to woodlands to grasslands, and locally to desertscrub. The current grassland connectors (grassland seas) between the mountain islands have been *in situ* approximately 9,000 years (Van Devender, 1990a,b; see references in Lowe, 1991).

The forested Chiricahua Mountains, rising to 9759 ft. (2975 m.), lie just south of the Madrean Line which divides the Madrean Archipelago into southern (Madrean) and northern (Rocky Mountain, or Petran) halves. The location of this sharp biogeographic line is, coincidentally, the same as that of highway 1-10 in southeastern Arizona and southwestern New Mexico.

"Mexican Mountain Rattlesnakes" in the genus *Crotalus* represent vertebrate taxa in forest and woodland communities in the Chiricahua Mountains--and other "Mexican Mountains" in the Madrean Archipelago--that illustrate the *northern* range limit for many Madrean (southern) taxa at and in the vicinity of the Madrean Line:

The Madrean-Petran Biogeographic Line
in Southeastern Arizona

Rocky Mountain
(Northern)

Santa Catalina, Rincon, Galiuro,
Winchester Mtns., et al.

C. viridis cerberus	Arizona Black Rattlesnake

N 4—

Sierra Madrean
(Southern)

Dos Cabezas, Chiricahua,
Huachuca, Santa Rita Mtns, et al.

C. pricei	Twinspotted Rattlesnake
C. *willardi*	Ridgenosed Rattlesnake
C. lepidus	Rock Rattlesnake

Rocky Mountain + Sierra Madrean
(Northern + Southern)

Pinaleno (Graham) Mountains

C. viridis cereberus	Arizona Black Rattlesnake
C. pricei	Twinspotted Rattlesnake

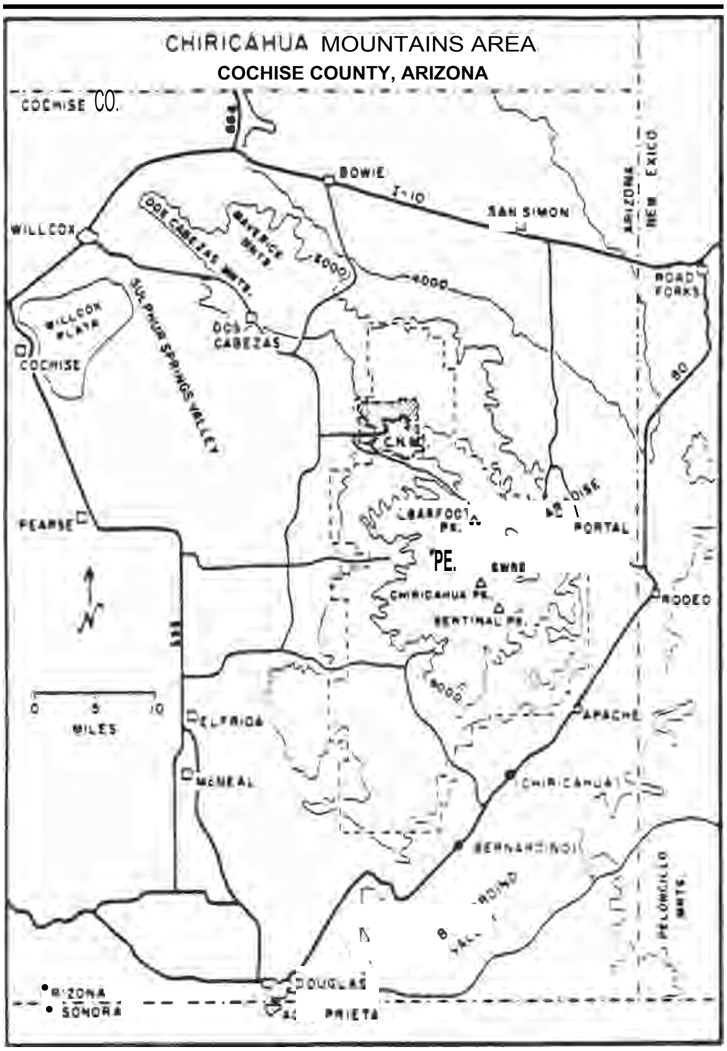


Fig. 1. The Chiricahua Mountains Area in the southeastern corner of Arizona.

The Arizona Black Rattlesnake *Crotalus viridis cerebus* exemplifies the *southern* limit for a northern taxon. As indicated above, both *C. v. cerberus* and the Twinspotted Rattlesnake *Crotalus pricei* of the Mexican Mountain group, occur in the Sierra Pinaleno (Graham Mountains) north of the Madrean Line.

Whereas the affinities of the montane fauna are largely on the south-north axis, lowland faunas lie at an east-west-south nexus. The range limits of several species and subspecies in or close to the Chiricahua Area support *this* biogeographic hypothesis: the Sonoran Desert Toad, widely distributed across southern Arizona, finds its eastern limit in the San Simon-San Bemadino valley system, as apparently does the Desert Tortoise; eastern and western subspecies of the Western Whiptail abut in low passes in the Peloncillo Mountains; *eastern* (Chihuahuan) and *southern* (Sonoran) subspecies of the Whipsnake meet in the San Bernadino Valley, whereas the *western* subspecies occupies the lowlands west of the Chiricahuas. The Plains Leopard Frog is at its westernmost range limit in the Sulpur Springs Valley. Many additional examples could be cited.

Like the Chiricahuan native fishes in forest and woodland streams, the native amphibians and reptiles in riparian systems are the most vulnerable among the threatened herpetofauna of the Chiricahua Mountains Area. The Chiricahua Leopard Frog and Plains Leopard Frog are the most threatened, followed by the Sonoran Mud Turtle and the Blacknecked Garter Snake. The authors would appreciate locality information for the observed occurrence of these and other species in the Chiricahua Mountains and surrounding areas, preferably accompanied by a photograph for documentation.

Literature Cited

Heald, W.F. 1951. Sky islands in Arizona. Nat. Hist., 60:56-63, 95-96.

Lowe, C.H. 1991. On the biogeography of the herpetofauna at Saguaro National Monument. *In* C.P. Stone and E.S. Bellantoni, eds, Proceedings of the symposium on research in Saguaro National Monument, Tucson.

Van Devender, T.R. 1990a. Late Quartenary vegetation and climate of the Chihuahuan Desert. *In* Betancourt et al., eds, Packrat middens, the last 40,000 years of biotic change. Univ. Arizona Press, Tucson.

Van Devender, T.R. 1990b. Late Quartenary vegetation and climate of the Sonoran Desert. *In* Betancourt et al., eds, Packrat middens, the last 40,000 years of biotic change. Univ. Arizona Press, Tucson.

Table 1. Amphibians and Reptiles of the Chiricahua Area.

- CLASS AMPHIBIA—The Amphibians
  - ORDER CAUDATA--Salamanders
    - FAMILY AMBYSTOMATIDAE—Mole Salamanders
      - Ambystoma tigrinum--Tiger Salamander (native?)
  - ORDER ANURA--Frogs and Toads
    - FAMILY PELOBATIDAE—Spadefoot Toads
      - Scaphiopus *bombifrons*--Plains Spadefoot
      - Scaphiopus couchi—Desert Spadefoot
      - Scaphiopus multiplicatus—Southern Spadefoot
    - FAMILY BUFONIDAE—True Toads
      - Bufo alvarius—Sonoran Desert Toad
      - Bufo cognatus--Great Plains Toad
      - Bufo debilis--Green Toad
      - Bufo *punctatus*--Redspotted Toad
    - FAMILY HYLIDAE--Treefrogs
      - Hyla arenicolor—Canyon Treefrog
    - FAMILY RANIDAE—True Frogs
      - Rana blairi—Plains Leopard Frog
      - Rana catesbeiana—Bullfrog (introduced)
      - Rana chiricahuensis—Chiricahua Leopard Frog
- CLASS REPTILIA—The Reptiles
  - ORDER TESTUDINES--Turtles
    - FAMILY KINOSTERNIDAE--Mud and Musk Turtles
      - Kinosternon sonoriense--Sonoran Mud Turtle
    - FAMILY EMYDIDAE—Box and Water Turtles
      - Terrapene ornata—Westem Box Turtle
    - FAMILY TESTUDINIDAE--Tortoises
      - Gopherus agassizi—Desert Tortoise (native?)
  - ORDER SQUAMATA—Lizards and Snakes
    - SUBORDER SAURIA—Lizards
      - FAMILY HELODERMATIDAE—Venomous Lizards
        - Heloderma suspectum—Gila Monster
      - FAMILY GEKKONIDAE--Geckos
        - Coleonyx *variegatus*--Western Banded Gecko
      - FAMILY IGUANIDAE—Iguanids
        - Cophosaurus texanus—Greater Earless Lizard
        - Callisaurus draconoides--Zebratailed Lizard
        - Crotaphytus collaris—Common Collared Lizard
        - Gambelia wislizenii—Leopard Lizard
        - *Holbrookia* maculata—Lesser Earless Lizard
        - Phrynosoma *cornutum*--Texas Homed Lizard
        - *Phrynosoma* douglassi—Short-homed Lizard
        - *Phrynosoma* modestum—Roundtailed Homed Lizard
        - *Phrynosoma* solare—Regal Homed Lizard
        - Sceloporus *clarki*--Clark Spiny Lizard
        - Sceloporus jarrovi—Mountain Spiny Lizard
        - Sceloporus magister—Desert Spiny Lizard

- Sceloporus scalaris--Bunchgrass Lizard
- Sceloporus undulatus--Eastern Fence Lizard
- Sceloporus virgatus—Striped Plateau Lizard
- Urosaurus ornatus--Tree Lizard
- Uta stansburiana--Side-blotched Lizard

- FAMILY SCINCIDAE–Skinks
  - Eumeces obsoletus--Great Plains Skink
- FAMILY TEIIDAE--Whiptails and Allies
  - Cnemidophorus exanguis–Chihuahuan Spotted Whiptail
  - Cnemidophorus inornatus—Little Striped Whiptail
  - Cnemidophorus sonorae--Sonoran Spotted Whiptail
  - Cnemidophorus tigris–Western Whiptail
  - Cnemidophorus uniparens--Desert-Grassland Whiptail
- FAMILY ANGUIDAE—Anguids
  - Gerrhonotus kingi–Madrean Alligator Lizard

- SUBORDER SERPENTES--Snakes
  - FAMILY LEPTOTYPHLOPIDAE—Blind Snakes
    - Leptotyphlops dulcis—Texas Blind Snake
    - Leptotyphlops humilis—Western Blind Snake
  - FAMILY COLUBRIDAE–Colubrids
    - Arizona elegans--Glossy Snake
    - Diadophis punctatus--Ringneck Snake
    - Elaphe triaspis--Green Rat Snake
    - Gyalopion canum–Chihuahuan Hooknosed Snake
    - Heterodon nasicus--Western Hognosed Snake
    - Hypsiglena torquata–Night Snake
    - Lampropeltis getulus--Common Kingsnake
    - Lampropeltis pyromelana--Sonoran Mountain Kingsnake
    - Masticophis bilineatus--Sonoran Whipsnake
    - Masticophis flagellum--Coachwhip
    - Pituophis melanoleucus—Bullsnake (Gopher Snake)
    - Rhinocheilus lecontei--Longnosed Snake
    - Salvadora grahamiae--Mountain Patchnosed Snake
    - Salvadora hexalepis—Westem Patchnosed Snake
    - Sonora semiannulata--Ground Snake
    - Tantilla hobartsmithi--Southwestern Blackheaded Snake
    - Tantilla nigriceps--Plains Blackheaded Snake
    - Tantilla yaquia--Yaqui Blackheaded Snake
    - Thamnophis cyrtopsis—Blacknecked Garter Snake
    - Thamnophis marcianus—Checkered Garter Snake
    - Trimorphodon biscutatus--Lyre Snake
  - FAMILY ELAPIDAE–Coralsnakes
    - Micruroides euryxanthus–Westem Coralsnake
  - FAMILY VIPERIDAE—Vipers
    - Crotalus atrox--Western Diamondback Rattlesnake
    - Crotalus lepidus--Rock Rattlesnake
    - Crotalus molossus--Blacktailed Rattlesnake
    - Crotalus pricei--Twinspotted Rattlesnake
    - Crotalus scutulatus–Mojave Rattlesnake
    - Crotalus viridis–Prairie Rattlesnake
    - Sistrurus catenatus—Massasauga

Laying Eggs or Giving Birth, The Amazing Reproductive Biology of Horned Toads.

Wendy Marlor
Department of Integrative Biology
Museum of Vertebrate Zoology
University of California, Berkeley
Berkeley, California 94720

Introduction

Viviparity, or live bearing, among vertebrates is a relatively common reproductive mode (Yaron, 1985). Yet, biologists have only recently begun to piece together the mechanisms and parameters underlying the factors associated with a shift from egg laying (oviparity) , the ancestral reproductive mode, to viviparity, the derived reproductive mode. Within squamates alone, there have been at least 90 independent shifts from oviparity to viviparity and, in a few cases, these shifts involve the development of a placenta. If viviparity has evolved frequently in squamates, is viviparity a "radical" change from oviparity?

I have been assessing characters involved in the evolution of viviparity within the monophyletic genus Phrynosoma. Montanucci (1987), utilizing both skeletal and muscular data, proposed a phylogeny (see table 1) that indicates the lineage diverged into northern and southern radiations. Most importantly, however, horned toads have independently evolved live bearing in each radiation, resulting in a total of four viviparous and eight oviparous species.

Four species of horned toads, P. douglassi, P. solare, P. cornutum and P. modestum, can be found within and/or proximate to the Chiricahua Mountains. This unusual density of horned toad species is further enhanced by the diversity in reproductive mode among the four species; P. douglassi is viviparous and the other three species in the area are oviparous. I have been collecting data concerning interspecific variation in reproductive organs such as ovaries, oviducts, uteri, placentas and extra-embryonic membranes and, variation in developmental parameters such as organ differentiation and growth. Developmental data, however, will not be included in this discussion due to limited space. Upon analysis of my data, I am hypothesizing that viviparity is a subtle alternative to oviparity in the genus Phrynosoma. My hypothesis is based on the following: the distribution of viviparity within the genus, the similarity of reproductive anatomy and extra-embryonic membrane morphology between oviparous and viviparous species, and, the unique body shape of both oviparous and viviparous species.

The distribution of viviparity in horned toads is best illustrated by Table 1 and noting where viviparity has evolved. For example, if viviparity evolved twice in the genus, the reproductive mode shift would have occurred near junction "E" and again near junction "B". If this scenario is correct, the branch of the phylogeny leading to the extant species P. taurus, has shifted reproductive modes twice, oviparity to viviparity then, viviparity to oviparity. An alternative interpretation of phylogeny is viviparity evolving three times. This scenario involves viviparity evolving near junction "E", along the branch leading to the extant species P. ditmarsi, and along the branch leading to the extant species P. braconnieri. Either interpretation regarding the distribution of viviparity and its evolution seems to indicate that the genus is dynamic with respect to reproductive mode.

The reproductive organs of female oviparous and viviparous horned toads were analyzed and compared. The ovaries are paired and located in the abdominal cavity against the dorsal body wall. Maternal yolk investment during the reproductive cycle, in both oviparous and viviparous species, was estimated as the mean diameter of ovarian follicles divided by the specimen's snout vent length. It was found that the yolk investment by P.douglassi was comparable to yolk investment of the three other oviparous species but, that the rate of follicle enlargement varied. Consequently, yolk investment per young does not change with reproductive mode shift. In addition, oviducal structures in oviparous and viviparous species were also analyzed. The oviducts are tightly oppressed against the dorsal body wall in all species of horned toads but vary in function depending on the reproductive mode. For example, in oviparous species, oviducts are the sites of shelling and consequent retention of pre-oviposited eggs. In viviparous species, on the other hand, oviducts are the site of incubation of developing embryos and fetuses. Regardless of reproductive mode, I delineated oviducts into three regions anterior, middle and posterior (Cuellar, 1966). The anterior region's primary function is to "catch" the ovum and, in oviparous species, begin encapsulating the fertilized embryo with shell membranes which, will eventually be impregnated with calcium deposits. The middle and posterior oviducal regions, on the other hand, function primarily as incubation chambers. Oviducts were removed from both oviparous and viviparous species at comparable stages of their reproductive cycles. 12 micron sections of the oviducts were made along the anterior to posterior axes and stained to elucidate epithelium and muscle tissue. Using a digitizer, representative sections of each of the three regions were analyzed for the following; epithelial surface area, muscularis mucosa and propria area, and degree of vascularization. Epithelial surface area and muscle area were estimated by measuring the surface area with the digitizer and dividing the number by the snout vent length of the animal. Vascularization was estimated by counting the number of capillaries in each region and dividing the number by the snout vent length. My results indicate that the anatomy of the oviducts in both oviparous and viviparous species of horned toads, do not differ significantly. Preliminary data concerning the density and distribution of oviducal glands, however, does seem to indicate that oviparous species have sparse glandular tissue and these glands seem to be concentrated in the anterior region of the oviduct. Glandular tissue in viviparous species, however, is more uniformly distributed along the anterior to posterior axis. Finally, I compared extra-embryonic membrane morphology between oviparous and viviparous species. My results indicate that the extra-embryonic membranes of viviparous species are more vascularized and are significantly more folded (higher surface area) than comparable membranes in oviparous species. Furthermore, the shell membranes in viviparous species are greatly reduced and/or missing as well as being void of mineral deposits. Additional work needs to be done to assess whether or not the extra-embryonic membranes in viviparous species are functionally different from their oviparous counterparts and/or may be analogous to the membranes of mammalian placentas. Consequently, the evolution of live bearing in horned toads does not seem to involve or require "radical" changes in maternal reproductive anatomy.

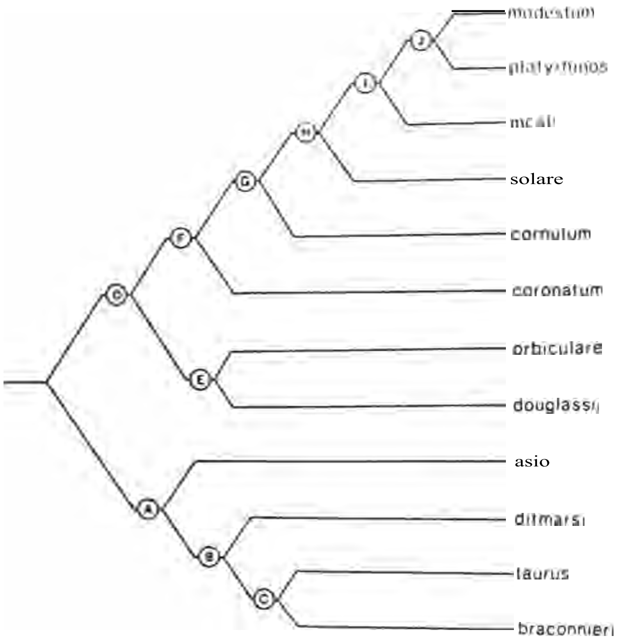
Lastly, all species of horned toads, regardless of reproductive mode, have a body shape ideal for carrying eggs (pre-oviposition) or developing fetuses. Furthermore, horned toads are cryptic and well-camouflaged appearing like "reproductive tanks" suitable for bearing large clutches. The consistency of a body plan suitable for oviparity or viviparity further strengthens my hypothesis that either reproductive mode seems to fit comfortably within the group's life history modes.

Conclusions and Further Research

It is this aspect, the variables involved in life history modes, that future research will yield clues regarding the types of selective pressures influencing variation in reproductive mode. Because the Chiricahuas offer a unique habitat of high horned toad species diversity, research within this area has the highest potential to yield pertinent data.

Table 1

Phylogenetic Relationships of Species Within the Genus *Phrynosoma* (Montanucci, R. 1987).



Literature Cited

Blackburn, D. (1982). Evolutionary origins of viviparity in the Reptilia. I. Sauria. Amphibia-Reptilia 3, 185-205.

Cuellar, 0. (1966). Ovidical anatomy and sperm storage structures in lizards. J. Morph. 119, 7-19.

Marlor, W. (1990). Comparative Oviduct Morphology of a Lineage of Reproductively Bimodal Iguanids, Genus *Phrynosoma.* American Zoologist, Vol. 30, Number 4.

Marlor, W. (1991). Extra-Embryonic Membrane Morphology and Comments on the Evolution of Viviparity in a Lineage of Reproductively Bimodal Iguanids, Genus *Phrynosoma.* X. International Symposium On Morphological Sciences, Toronto, Canada, July 1991

Montanucci, R. (1987). A Phylogenetic Study of the Horned Lizards, Genus *Phrynosoma,* Based on Skeletal and External Morphology. Contributions in Science, No. 390, Dec. 19, 1987. Natural History Museum of Los Angeles County.

Yaron, Z. (1985). Reptilian placentation and gestation: Structure, function and endocrine control. In C. Gans and F. Billet (eds): Biology of the Reptilia, Vol. 15. New York: Wiley, pp. 527-603.

GENETIC VARIATION AND HISTORICAL DISTRIBUTION PATTERNS IN POPULATIONS OF YARROW'S SPINY LIZARD, *Sceloporus jarrovi*

G.A. Middendorf and J.S. Frankel
Department of Zoology, Howard University, Washington, DC 20059

Introduction

With some 70 species distributed throughout central and north America, *Sceloporus* is thought to be the second most specious genus of the family Iguanidae. While subjected to a number of taxonomic studies over the years, the origins, relationships and biogeography of the genus remain unsettled (compare for instance Smith, 1939; Chrapliwy, 1964; Etheridge, 1964; Larsen and Tanner, 1975).

Because its range extends into the US, one of the most studied species in the genus is the mountain or Yarrow's spiny lizard, *Sceloporus jarrovi.* This "sky-island" species is moderate-sized (maximum snout-vent about 100 mm for males; slightly less for females) and lives at elevations between 1500 and 3000 m. Eight subspecies, ranging from southern Arizona and New Mexico through the Sierra Madre Occidentals to western Guanajuato and Queretaro, have been recognized. These are hypothesized to have arisen as the result of population expansion and isolation during the glacial epochs of the Pleistocene; presumably, after spreading across the cooler desert valleys during glacial advances, populations became isolated from one another as they retreated to the mountaintops during the interglacial periods. More localized fractionation within populations may have also occurred, resulting in the present mountaintop distribution within a desert sea.

In Arizona and New Mexico, at the northern end of its range, S. jarrovi has been reported from the Animas, Boboquivari, Chiricahua, Dos Cabezas, Dragoon, Graham (Pinaleno), Hatchet, Huachuca, Peloncillo, Pyramid, Quinlan, San Luis, and Santa Rita Mountains (Stebbins, 1985). At lower elevations within these ranges the lizards occur primarily on rocks and rock faces near riparian habitats, higher up they prefer cliff faces and talus slopes. Regardless of elevation, lizard distribution appears to be limited by the availability of crevices in these rocky areas where they congregate and overwinter. In the spring, individuals disperse from these hibernacula, establish territories, give birth in late May through June, and then mate in September and October before returning to the hibernacula (Fitch, 1970; Ruby, 1977; Congdon et al., 1979; Simon and Middendorf, 1980).

Once they have established territories as juveniles, the lizards generally exhibit high site fidelity, often returning to the same area in subsequent years (Middendorf, unpublished data). Although migration and displacement (during the process of establishing territories) both occur, wide-ranging dispersal is unlikely; animals are limited by the lack of both acceptable summer and winter sites. At lower elevations canyons serve as corridors of movement (animals are rarely found in the drier, more open areas between drainages), while at higher elevations ridges and rocky outcrops act similarly. Habitat requirements and behavioral adjustments to varying levels of resources and population density effectively restrict and reduce the direction and distance individuals are likely to move (Simon and Middendorf, 1976; Middendorf, 1984; Middendorf and Simon, 1988). Thus, annual movement occurs within corridors connecting summer territories and winter hibernacula. If we view hibernacula as the foci for the "deme," gene flow will be seen to occur only when hibernacula are near enough to one another that individuals from different "demes" establish adjacent territories, e.g. only where edges of different hibernacula groups overlap during the breeding season. Thus, within a mountain range, patterns of gene flow will be linear or web-like in nature-- connected along the ridges and peaks, individual strands will descend down canyons where to end at the lower elevations.

Thus, S. jarrovi. populations are expected to be comprised of numbers of inbred demes, e.g. a metapopulation structure (Hansson, 1991), delimited by a combination of site fidelity, lizard mobility within acceptable microhabitats, and the spacing of hibernacula sites. In fact, because of these conditions, subpopulations should largely be delimited by zones of limited contact within migration corridors.

A number of predictions regarding population structure follow. For instance, at lower elevations genetic variability between adjacent canyons should be greater than within a canyon system - almost irrespective of the distances involved. Genetic differences between adjacent canyons at the higher elevations should be less than at lower elevations. Variation should be directly affected by distance between hibernacula. Similar but even stronger predictions should hold for genetic distance and variability between populations in different mountain ranges.

The success of application of isozyme profiles and patterns for obtaining evolutionary information, and for the elucidation of the amount of genetic variability within and among species has been well documented (e.g. Frankel and Underhill, 1974). And while several species of Sceloporous have been characterized with respect to inter- and intrapopulational genetic (allozymic) variation (for instance, S. grammicus) virtually no data has been compiled on similar parameters in S. jarrovi. Indeed, most of the work on this species has focused on attributes related to life history strategies, e.g. behavior, demography, ecology, physiology, and reproduction. The lack of knowledge regarding variables affecting the historic patterns of distribution and movement of S. jarrovi strongly limits our ability to develop effective management and conservation programs- of this as well as other similarly distributed species.

Present Studies

We are currently determining distribution patterns of *Sceloporus jarrovi* in southeastern Arizona and southwestern New Mexico. To do this, we are mapping hibernacula locations and dispersal boundaries, collecting tissue samples from lizard populations between different mountains and within ranges as defined by topographic and microhabitat features, and analyzing samples to determine variation in allozymic expression and levels of heterozygosity. By examining allele frequencies of S. jarrovi within this geographic area we will be able to 1) characterize genetic variability between and within collection sites, 2) define populations, and 3) using statistical and cladistical analysis, delineate historical relationships and patterns of movement.

Thus far we have examined muscle esterase phenotypes exhibited by S. *jarrovi* from 25 localities in the Chiricahua, Huachuca, Santa Rita, and Pinaleno Mountains. Analyses reveal four seperable zones of activity. Electropherograms of lizards from the Chiricahua and Huachuca locations were similar, exhibiting either of two different phenotypes, which differed from the phenotype exhibited by all lizards from the Santa Ritas and Pinalenos (Frankel and Middendorf, 1991). Our data suggest affinities between the Chiricahua and Huachuca populations and between the Santa Rita and Pineleno populations. Founder effects or subsequent drift could account for our observations, as well possibly explaining as morphological and color pattern variation (Middendorf, unpublished observations).

We also examined genetic variation for four other enzyme systems: LDH, MDH, MPI, and PGM. Of these, both LDH and MDH exhibited two loci so that six loci in all were assayed. While PGM and MPI were variable, LDH-A and MDH-A showed little variation and LDH-B and MDH-B exhibited no variation. Analysis of genetic variation of these enzyme systems for S. *jarrovi* populations in the Chiricahua and Huachuca Mountains using Wright's F statistic revealed no clear differetiation between ranges. Analysis of variation within each of the ranges also provided no support for the existence of barriers to gene flow. Chi-square heterogeniety tests did, however, suggest some genetic differences between ranges, but cannot be used to infer patterns of gene flow since the observed differences could just as well be the result of local selection pressures or random variation.

The exact relationships among the populations of S. *jarrovi* remain unclear. We are now examining additional enzyme systems in samples from these locations, as well as collecting samples from lizards in other ranges. These additional data should help resolve historical relationships and patterns of movement.

References

Chrapliwy, P.S. 1964. Taxonomy and distribution of the *jarrovi* complex of lizards of the *torquatus* group, genus *Sceloporus*. Ph.D. Thesis, University of Illinois, Urbana, IL.

Congdon, J., R.E. Ballinger, and K.A. Nagy. 1979. Energetics, temperature and water relationships in winter aggregated *Sceloporus* jarrovi (Sauria: Iguanidae). Ecol. 60(1):30-35.

Etheridge, R. 1964. The skeletal morphology and systematic relationships of sceloporine lizards. Copeia 1964(4):610-631.

Fitch, H.S. 1970. Reproductive cycles in lizards and snakes. Univ. Kansas Mus. Nat. Hist. Misc. Pub. 52, pp. 1-247.

Frankel, J.S. and G.A. Middendorf. 1991. An electrophoretic study of genetic variation in populations of Yarrow's spiny lizard *Sceloporus jarrovi* (Sauria, Iguanidae) - I. Esterase characterization and polymorphism. Comparative Biochemistry and Physiology 100B:173-176.

Frankel, J.S. and D.K. Underhill. 1974. Kidney esterase and serum albumin polymorphisms in four populations of the green grog Rana *clamitans*. Bull. N.J. Acad. Sci. 19:39-41.

Hansson, L. 1991. Dispersal and connectivity in metapopulations. Biol. J. Linnean. Soc. Lond. 42:89-103.

Larsen, K.R. and W.W. Tanner. 1975. Evolution of the sceloporine lizards (Iguanidae). Great Basin Nat. 35(1):1-20.

Middendorf, G.A. 1984. The effects of population density on patterns of resource utilization by Yarrow's spiny lizard. J. Wash. Acad. Sci. 74(2):51-60.

Middendorf, G.A. and C.A. Simon. 1988. Thermoregulation in the iguanid lizard *Sceloporus jarrovi*: the influences of age, time, and light condition on body temperature and thermoregulatory behaviors. Southwestern Nat. 33(3):347-356.

Ruby, D.E. 1977. Winter activity in Yarrow's spiny lizard, *Sceloporus* jarrovi. Herpetologica 33(3):322-333.

Simon, C.A. and G.A. Middendorf. 1976. Resource partitioning by an iguanid lizard: temporal and microhabitat aspects. Ecol. 57(6):1317-1320.

Simon, C.A. and G.A. Middendorf. 1980. Spacing in juvenile lizards (*Sceloporus* jarrovi). Copeia 1980:141-146.

Smith, H.M. 1939. The Mexican and Central American lizards of the genus *Sceloporus*. Field Mus. Nat. Hist. Zool. Ser. 26:1-397.

LIMITING FACTORS AND MANAGEMENT STRATEGIES FOR GOULD'S TURKEYS IN THE PELONCILLO MOUNTAINS, NEW MEXICO

Sanford D. Schemnitz
Department of Fishery and Wildlife Sciences
New Mexico State University, Las Cruces, NM 88003

Introduction

The first description of the Mexican turkey was made by Gould (1856) and later substantiated by Nelson (1900). Gould's and Mexican turkey are synonymous names. The first known New Mexico specimen of Mexican turkey *(Meleagris gallopavo mexicana)was* an adult female collected May 31, 1892, by E.A. Meams and Holzner along the west side of the San Luis Mountains south of the Animas Mountains near the Mexican boundary in Hidalgo County. Two other birds, an adult female and male, were collected by Mearns (1907) in the same general locale. Another authentic specimen, an adult female, was collected May 16, 1957, by Bohl and Gordon (1958) in the Peloncillo Mountains 2½ miles east of the Arizona border, 7½ miles north of the Mexican border, and 1 mile west of the Pendleton Ranch. The identity of this bird was verified by Dr. A. S. Leopold and now resides in the Museum of Zoology, University of California, Berkeley collection. The New Mexico population is at the extreme northern edge of Gould's turkey range, which extends southward into Chihuahua, Mexico.

Schorger (1966) explored the historical distribution of *mexicana* in Arizona and concluded that no proof exists for past presence *of mexicana* in Arizona. One specimen collected in the Chiricahua Mountains in 1881 was verified as *merriami* by A.S. Leopold. Currently, the Chiricahua Mountains are occupied by a low density population of *merriami* originating from introductions in the 1930's and 1950's. Potentially, suitable habitat for Gould's extends westward along the international boundary as far west as Tumacacori Mountains, south of Tucson, and includes the Huachuca, Galiuro, and Patagonia Mountains. Presently, Gould's (Mexican) turkey is listed in New Mexico as a Group II (species whose prospect of survival within the state may be in jeopardy in the foreseeable future), endangered species. The subspecies is not listed as endangered in Arizona. Past information on the bird's status has been vague and sketchy. Low turkey populations in the past were suggested by Marshall (1957) who spent 18 days censusing birds in Clanton Canyon, Peloncillo Mountains, 1951 to 1955 and did not observe any wild turkeys. He also did not observe turkeys in the Turkey Canyon area of the San Luis Mountains, Chihuahua, in 8 days.

Leopold (1948, 1959) documented in detail the status of wild turkeys in Mexico. He mentioned a population of 1 bird per 60 acres in virgin pine-oak-juniper habitat in Chihuahua in 1937. By 1948 this population had increased to about 1 bird per 20 acres. Nevertheless, Leopold expressed concern over shrinkage of occupied turkey range in Mexico due to timber clearing and unrestricted hunting.

The objectives of our research have been (1) determine status, distribution, and abundance of Gould's turkeys in the Peloncillo Mountains, Coronado National Forest, New Mexico; (2) describe food habits; (3) describe occupied habitats and key habitat components; (4) monitor movements and determine activity patterns; (5) determine main limiting factors and suggest management practices.

Taxonomy

An adult male, 20 pound Gould's turkey was called in and captured in Whitmire Canyon on April 9, 1982. The gobbler was accompanied by 7 hens. Detailed measurements were recorded. The captured gobbler was photographed and typical feathers collected. The bird closelymatched the description by Ridgway and Friedmann (1946) of the coloration on the lower back and rump of the **M. g.** *mexicana* turkey as reddish and greenish with golden metallic reflections and not bluish black as in Merriam's turkey. Aldrich (1967) and Rea (1980) mentioned the white tips of the rectrices **M.** *g. mexicana* versus buff-tipped rectrices **M. g.** *merriami.* The captured bird had white tips. Another key characteristic of our captured bird that matched the descriptions by Lee (1959) and

Aldrich (1967) was the less evenly barred, more marbled and speckled tail feathers in contrast to the barring of **M. g.** mariami. The outer secondaries of the captured bird had broader white edgings and much less rufescent inner secondaries than **M. g.** merriami (Schorger, 1966). A unique characteristic of this adult gobbler was the lack of leg spurs.

Habitat and Life History

Grazing by domestic livestock is the dominant land use affecting the habitat, although some scattered fuelwood cutting (primarily fallen dead trees) occurs in oak bottoms in accessible areas.

Characteristic vegetation comprising the principal observed breeding range of Gould's turkey in the Peloncillo Mountains is classified by Brown et al. (1979) and Moir (1979) as the Madrean Evergreen Forest and Woodland Community and the Piñon-Juniper Woodland Community. The Madrean Evergreen Forest is dominated by evergreen oaks on alluvial fans, or on alluvial soils in canyon bottoms. These oaks are typically on lower slopes or riparian communities intermingled with oak-pine, piñon-juniper, interior chaparral, shrub steppe, and piedmont desert grasslands on the upland sites.

Three riparian habitat types, made up 4.5% of the area used by turkeys accounted for 71.5% of all observations. The mean hatching date from 1982 to 1988 was 20 June.

Roost Sites

Potter et al. (1985) reported 16 roost sites in 1983. The number of active roost sites has increased to 38 in 1990. Similarly, the number of trees per roost increased from 3 trees/site in 1983 to 5. roost trees/roost site in 1990. Trees at 26 of the roost sites (84%) were Chihuahua pine (*Pinus leiophylla*). Emory oaks (*Quercus emoryi*) were used at 5 roost sites (16%). Other tree species used less frequently included sycamore (*Platanus wrightii*), Fremont cottonwood (*Populus fremonti*), and Arizona walnut (*Juglans major*). Roost sites have been documented in 13 (68%) of 19 Chihuahua pine stands in the study area. The Chihuahua pine-silverleaf oak habitat comprised 1.1% of the study area. A characteristic feature of the occupied trees was the presence of one or more horizontal limbs free from dense sprout branches offering suitable perches for roosting. Gould's turkey resemble the Rio Grande subspecies in certain aspects of their habitat needs. Both subspecies readily utilize riparian habitat and roost in deciduous trees.

Population Status

Recent Gould's turkey research in New Mexico was begun in 1982 (Potter et al. 1985). Initial population was 12 birds, but has increased annually to 75 turkeys in 1988 (Table 1). Adult males have increased from 1 in 1983 to 18 in 1988. Gould's turkey range has increased from 3,600 ha in 1983 to 7,200 ha in 1986 and 13,000 ha in 1988. A flock of 24 turkeys, the largest documented Gould's winter flock in the United States, was seen 26 February 1988. Annual precipitation was above average each year, 1982-1988, and 27% above the long-term average. This above-normal rainfall contributed to lush vegetation and may partially explain the population increase.

Table 1. Known population numbers and structure, 1983, and estimated population numbers and structure, 1985 through 1988 of Gould's turkeys in Peloncillo Mountains, New Mexico.

Age and sex	1983	1985	1986	1988
Adult male	1	9	10	18
Adult female	2	**4**	5	14
Subadult	3	6	13	9
Poult	6	16	17	34
Totals	12	35	45	75

Limiting Factors and Threats to Survival

Specific limiting factors for Gould's turkey are unknown. Hubbard et al. (1977) suggested lack of water, predators and poaching as threats to survival in the Animas Mountains. Mountain lions are abundant in the Peloncillo Mountains. Ten were taken by New Mexico Department of Game and Fish personnel on the Pendleton Ranch, approximately 9,000 acres, during 1981-1982. We documented mountain lion predation on Gould's turkeys. A danger to existing Gould's turkey populations in the Peloncillo Mountains is potential hybridization with domestic turkeys. A wild hen mated with a domestic gobbler and raised 7 poults at the Guadalupe Canyon Ranch headquarters, 1 mile south of the Coronado Forest boundary, in 1976 (D. Hadley, pers. commun.). Numerous hybrid offspring have resulted from this mating. Poaching and competition from feral hogs are other adverse factors.

Management Strategies

Aldrich (1946) commented that, "No intelligent wildlife manager ignores the difference between species of birds in his management practices. Too often, however, differences between races have been ignored, usually with unfortunate results". Aldrich continued, "It seems obvious that stocking with a foreign race is a waste of time and money, at least while any of the original inhabitants of a region still survive. Instead of introducing new birds of a strange race, the original occupants of the region should be given every encouragement to increase their population to the carrying capacity of the region". Hopefully any efforts to augment existing Mexican turkeys will be based on stocking pure, i.e. mexicana birds. No repetition of previous stocking of Merriam's turkey, as in the past, should be attempted. We suggest that the hybrid domestic-mexicana turkeys in Guadalupe Canyon be eliminated. The landowner has destroyed some of the hybrid birds. The landowner might be persuaded to kill the entire flock if the turkeys could be replaced with wild Gould's, and we strongly suggest this action.

The riparian habitats in the Peloncillo Mountains are critical to the turkeys'survival. They contain the majority of the feeding, roosting, and brood-rearing sites, as well as travel lanes for the turkeys. We suggest that the bulk of the management effort should be spent protecting and enhancing these areas. Due to the low precipitation in the area, permanent water sources should be established in these riparian habitats. The New Mexico Chapter, National Wild Turkey Federation in cooperation with the U.S. Forest Service has built 3 rock-header dams in the area, but additional ones are needed. These dams are designed to seep slowly to provide succulent vegetation below the dam as well as a permanent water supply.

The Chihuahua pine-silverleaf oak habitat comprises only 1.1% of the total area, yet it includes most of the suitable roost sites. With plantings of sycamore and cottonwood, we could increase diversity and create new roost sites. These plantings should be done near established permanent water sources to provide cover. Finally, seasonal reductions or total exclusion of livestock, and experimental controlled burns should be used to rejuvenate degraded riparian habitats.

Future research should investigate the causes of low turkey populations in the Chiricahua Mountains.

Acknowledgements

I am indebted to the U.S. Forest Service, New Mexico Department of Game and Fish, New Mexico State University Agricultural Experiment Station, National and New Mexico Chapter, Wild Turkey Federation for financial support of my research. I thank Gary Helbing, Tom Skinner, Randall Smith and Bill Zeedyk of the U.S. Forest Service for their interest and support. I am grateful to wildlife graduate students, Dan Figert, Tom Potter, Bob Willging, Darryl York and Mark Zomes for their dedicated hard work on this turkey project.

Literature Cited

Aldrich, J.W. 1946. Significance of racial variation in birds to wildlife management. J. Wildl. Manage. 10:86-93.

Aldrich, J.W. 1967. Taxonomy, distribution, and present status. Pages 17-44 in: O.H. Hewitt (ed.). The wild turkey and its management. The Wildlife Society. Washington, D.C. 589 p.

Bohl, W.H. and S.P. Gordon. 1958. A range expansion of Meleagris gallop== mexicanaFiredman into southwestern New Mexico. Condor 60:338-339.

Brown, D.E., C. H. Lowe, and C.P. Pase. 1979. A digitized classification system for the biotic community (series) and association examples for the Southwest. J. Arizona-Nevada Acad. Sci (Suppl. 1) 14:1-14.

Gould, J. 856. On a new turkey, Meleagris mexicana. Proc. Zool. Soc. London 24:61-63.

Hubbard, LP., M.C. Conway, C.G.Schmitt, and M.D. Hatch. 1977 **A** biological inventory of the Animas Mountains. Hidalgo County. New Mexico. New Mexico Department of Game and Fish, Santa Fe. 56 p.

Lee, L. 1959. The present status of the wild turkey in New Mexico. Proc. Natl. Wild Turkey Symp. 1:11-18.

Leopold, A.S. 1948. The wild turkeys of Mexico. Trans. N. Am. Wildl. Conf. 13:3939-400.

Marshall, J.T., Jr. 1957. Birds of pine-oak woodland in southern Arizona and adjacent Mexico. Pacific Coast Avifauna 32. 128 p.

Mearns, E.W. 1907. Mammals of the Mexican boundary of the United States. U.S. Natl. Mus. Bull. 56 530.

Moir, W.H. 1979. Soil-vegetation patterns in the central Peloncillo Mountains, New Mexico. **Am.** Midl. Nat 102:317-331.

Nelson, E.W. 1900. Description of a new subspecies of Meleagris gallopam and proposed changes in the nomenclature of certain North American birds. **Auk** 17:120-126.

Potter, T.D., S.D. Schemnitz and W.D. Zeedyk. 1985. Status and ecology of Gould's turkey in New Mexico. Proc. Natl. Wild Turkey Symp. 5:1-24.

Rea, A.M. 1980. Late Pleistocene and Holocene turkeys in the southwest. Contrib. Sci. Nat. Mus Los Angeles 330:209-224.

Ridgway, R., and H. Friedmann. 1946. The birds of North and Middle America. Part 10, U.S. Nat. Mus. Bull. 50. 484.

Schorger, A..W. 1966. The wild turkey: its history and domestication. Univ. Oklahoma Press, Norman. 625 p.

HORNY "TOAD" TALES FROM THE CHIRICAHUA MOUNTAINS, AS TOLD BY A BIOLOGIST

Wade C. Sherbrooke
Southwestern Research Station
American Museum of Natural History
Portal, Arizona 85632

I began studying horned lizards (horny toads; genus *Phrynosoma*) in the Chiricahua Mountains and surrounding valleys in 1976. The genus is found from southern Mexico to southwestern Canada, with thirteen species currently recognized in North America. Of the seven species found in the United States, four occur in the vicinity of the Chiricahua Mountains (Sherbrooke 1981): Texas horned lizard, *Phrynosoma cornutum*; round-tailed horned lizard, *Phrynosoma modestum*; mountain, or short-horned, horned lizard, *Phrynosoma douglassii;* regal horned lizard, *Phrynosoma solare.* Additional species occur just south of the Chiricahua Mountains in the Sierra Madre Occidental of western Mexico, i.e., the rock horned lizard, *Phrynosoma ditmari.*

Horned lizards are a distinct—morphologically, ecologically, and behaviorally—assemblage of species of iguanid lizards that are evolutionarily separate from other genera. They are feeding specialists on ants, although they do not require ants in their diet (Sherbrooke 1987a). They are extremely cryptic in color and pattern (Sherbrooke 1981; Sherbrooke and Montanucci 1988), are slow runners of large body girth, and have a number of specialized defensive behaviors and an integumental morphology to deter predators (Sherbrooke 1988a, 1988b, 1990a, 1991; Middendorf and Sherbrooke 1992). Other aspects of their biology, such as color changes associated with thermoregulation, are more typical of desert iguanids (Sherbrooke 1988a; Sherbrooke and Frost 1989).

The habit of eating ants, particularly harvester ants of the genus *Pogonomyrmex*, exposes horned lizards to potential stings, involving injection of the potent venom of these hymenopterans. We have discovered that the blood plasma of horned lizards is able to detoxify the venom of harvester ants (Schmidt, Sherbrooke, and Schmidt 1989). Apparently this is a biochemical adaptation associated with their dietary specialization. Harvester ants serve as secondary hosts for an intestinal nematode, *Skrjabinoptera phrynosoma,* which exhibits a unique life cycle (Sherbrooke 1981; M.D. Stuart and W.C. Sherbrooke, MS in preparation). Horned lizards purposefully ingest pebbles that may serve to crush ant prey, dislodge stomach nematodes, or act as a source of minerals (Sherbrooke 1987a).

Drinking water is often difficult to acquire for lizards living in the dry habitats surrounding the Chiricahua Mountains, a classic survival challenge for a desert organism. Texas horned lizards have perfected a unique method for capturing even tiny raindrops for drinking. They employ what I have termed "rain-harvesting," a stereotyped behavioral posture combined with dorsal scale features of their integument (Sherbrooke 1990b). In a light rain a lizard will arch its back upwards, spread its back and legs laterally, and drink water collected from its upper surface. Intercepted water spreads over the integument through interscalar capillary channels to the mouth for ingestion.

The skin also plays an important role in thermoregulation, darkening when the animal is cold and lightening when it is hot (Sherbrooke 1988a, 1988b; Sherbrooke and Frost 1989). This physiological color change is regulated hormonally (a-MSH) and by neurotransmitters (ß-adrenoceptors) (Sherbrooke 1988a), which regulate the distribution of pigment granules (melanosomes) of melanophores within the dermis. The architectural arrangement of pigment cell types allows rapid darkening and lightening of the animal's color.

This physiological color change is distinct from the different color forms inhabiting different geographic areas, which are associated with crypticity (Sherbrooke and Montanucci 1988). We are currently studying the biochemical basis of a color polymorphism in *Phrynosoma modestum* populations near Portal that apparently involves diffei7ences in pterin pigments in xanthophores and erythrophores (Sherbrooke and Frost 1989). These color polymorphic, stone-mimicking lizards, are seemingly exhibiting aspect diversity as an evolutionary strategy to thwart the ability of predators to develop effective search images (Sherbrooke and Montanucci 1988).

We have also discovered that the skin of horned lizards contains an abundance of intraepidermal mechanoreceptors, the ultrastructural components of which we have described (Sherbrooke 1988a; W.C. Sherbrooke and **R.B.** Nagle, MS in preparation). I am continuing behavioral studies to determine their functional significance to the lizards.

Lacking the strong territorial urges found in many iguanid lizards, horned lizards exhibit unique social behaviors. Upon meeting, two lizards interact by one presenting its vent (with its tail raised) and the second licking the first lizard's vent region—these behaviors are termed "vent-flashing" and "vent-licking" (Sherbrooke 1988a). These social behaviors appear to be part of an overall strategy of minimizing visual advertisement to avoid predation. We have demonstrated that the odor of one lizard can be detected by another (C.A. Simon and W.C. Sherbrooke, MS in preparation).

The horns, scaly skin, and numerous behaviors of horned lizards all are employed in attempts to dissuade potential predators from eating horned lizards if they have been found and caught. They have a variety of predators (Sherbrooke and Montanucci 1988), some of which must swallow their prey whole. Snakes may be deterred by the horns-forward response of many species (Sherbrooke 1987b), while a variety of other behaviors—several designed to increase the apparent or real size of the lizard—are utilized in encounters with roadrunners, *Geococcyx californianus* (Sherbrooke 1990a), and grasshopper mice, *Onychomys torridus* (Sherbrooke 1991).

Perhaps the most bizarre behavior of horned lizards, one only infrequently seen, is their ability to propel a stream of blood from blood sinuses surrounding the eyes. Known since 1871, the phenomenon has remained little studied. Four years ago we began to systematically evaluate the hypothesis that it is a defensive mechanism to deter predation by canids. Using a dog, *Canis familiaris*, we have shown blood squirting in a high percentage of trials (70%-100%). This suggests, especially when put into the context that blood is not squirted at other potential predators (Sherbrooke 1990a, 1991), that the response is predator specific. We have demonstrated that it functions at various temperatures, day or night (Middendorf and Sherbrooke 1992), and that repeated squirting bouts involve large losses of blood (W.C. Sherbrooke and G.A. Middendorf, MS in preparation). We are currently involved in chemical analysis of squirted versus systemic blood and behavioral trials of the response of canids to the blood.

The diversity of species of horned lizards found near the Chiricahua Mountains is unique, providing research opportunities that are only beginning to be realized. This is indicative of the research significance of the biota of the mountain and desert areas of southeastern Arizona, a region of extremely high biodiversity in the United States.

Literature Cited

Middendorf, G.A. and W.C. Sherbrooke. 1992. Canid elicitation of blood-squirting in a horned lizard (Phrynosoma cornutum). Copeia 1992:519-527.

Schmidt, P.J., W.C. Sherbrooke, and J.O. Schmidt. 1989. The detoxification of ant (Pogonomyrmex) venom by a blood factor in horned lizards (Phrynosoma). Copeia 1989:603-607.

Sherbrooke, W.C. 1981. Horned lizards: unique reptiles of western North America. Southwest Parks and Monuments Association, Globe. Popular Series No. 31,48 pp.

Sherbrooke, W.C. 1987a. Captive Phrynosoma solare raised without ants or hibernation. Herpetological Review 18:11-13.

Sherbrooke, W.C. 1987b. Defensive head posture in horned lizards (Phrynosoma: Sauria: Iguanidae). Southwestern Naturalist 32:512-515.

Sherbrooke, W.C. 1988a. Integumental biology of homed lizards (Phrynosoma). Ph.D. Dissertation, University of Arizona, Tucson, 220 pp.

Sherbrooke, W.C. 1988b. Homed lizard integument—an organ exposed. Tucson Herpetological Society Newsletter 1(11):95-99.

Sherbrooke, W.C. 1990a. Predatory behavior of captive Greater Roadrunners on adult horned lizards. Wilson Bulletin 102:171-174.

Sherbrooke, W.C. 1990b. Rain-harvesting in a lizard, Phrynosoma cornutum: behavior and integumental morphology. Journal of Herpetology 24:302-308.

Sherbrooke, W.C. 1991. Behavioral (predator–prey) interactions of captive grasshopper mice (Onychomys torridus) and horned lizards (Phrynosoma cornutum and P. modestum). American Midland Naturalist 126:187-195.

Sherbrooke, W.C. and S.K. Frost. 1989. Integumental chromatophores of a color-change thermoregulating lizard, Phrynosoma modestum (Iguanidae: Reptilia). American Museum Novitates (2943):1-14.

Sherbrooke, W.C. and R.R. Montanucci. 1988. Stone-mimicry in the round-tailed horned lizard Phrynosoma modestum (Sauria: Igaunidae). Journal of Arid Environments 14:275-284.

SUPERNUMERARIES AT BUSHTIT (PSALTRIPARUS MINIMUS) NESTS IN THE CHIRICAHUA MOUNTAINS: INCIDENCE, ORIGINS, AND PROXIMATE CAUSES

Sarah A. Sloane
Bird Division, Museum of Zoology
The University of Michigan, Ann Arbor, MI 48109 *

Cooperative breeding systems are social systems in which some individuals behave parentally toward offspring that are not their own. These 'helpers' appear to act altruistically, incurring a cost to their own fitness while increasing the fitness of the individuals they help. The evolution of this behavior has been the subject of debate ever since Darwin (1859) presented it as problematic to his theory of evolution through natural selection. In the 1960's additional theories designed to address this problem were developed, in particular the concept of inclusive fitness (Hamilton 1964). These new ways of viewing an old problem stimulated intense research on cooperative social systems, especially those of birds (for reviews, see Emlen and Vehrencamp 1983, Brown 1987, Stacey and Koenig 1990).

The bushtit *(Psaltriparus minimus)* has the distinction of being one of the three birds first described as having 'helpers at the nest' in Alexander Skutch's (1935) landmark paper on that subject. Since then, however, little research has been conducted on these interesting little birds, possibly because their small size (averaging 6 grams) has intimidated many would-be researchers. Bushtits are actually in many ways ideal for the study of avian cooperative breeding. For example, they are common and distributed widely throughout much of the western US, making them a relatively accessible study organism. Most important however, bushtits appear to vary geographically in the proportion of nests with helpers: from common in the highlands of Guatemala (Skutch 1935) to rare, and perhaps even anomalous, in southern California (Ervin 1977). Proximate factors influencing the expression or suppression of helping behavior may reflect past selective factors important in its evolutionary history.

From 1986 through 1991, I studied the ecology and behavior of a population of bushtits in the Chiricahua Mountains. The study site is located, at an elevation of approximately 1700-1800 meters, in the Cave Creek basin of the Chiricahua Mountains within the Coronado National Forest, 7 km from the town of Portal, Cochise County, Arizona and approximately 2 km from the Southwestern Research Station of the American Museum of Natural History. It is a gently sloping xeric area cut by two deep riparian gorges. The predominant vegetation throughout the study area is open oak woodland grading into pine-oak woodland. I caught and individually marked over 700 nestling, juvenile (i.e. birds hatched earlier in the season) and adult bushtits. In all years, except 1986, the study was conducted during the entire bushtit breeding season (early March through late July). Although the majority of my research involved field observations, I supplemented these with an aviary experiment in which I tested the effects of food supply arid helper condition on the response of individuals to the sound of begging nestlings

The primary goals of my research were to 1) document the extent of multibird (>2 bird) nests and variations in the social system, 2) determine the ecological factors influencing inter-nest and inter-individual variation in nest-joining and associated competitive behavior patterns, and 3) develop an evolutionary scenario to explain the social complexity that I found.

Description of social structure

I found the social system of bushtits in the Chiricahua Mountains to be complex and variable (see Sloane 1992). During the breeding season, bushtits lived in flocks of 20-40 individuals, forming pairs within flocks at the beginning of the breeding season. About one-third of the 200 nests observed had supernumeraries (Figure 1). These birds were primarily adult males, but some adult females and four juveniles were observed as extra attendants at nests. Supernumeraries were usually failed breeders from earlier or concurrent nests or they were unmated males.

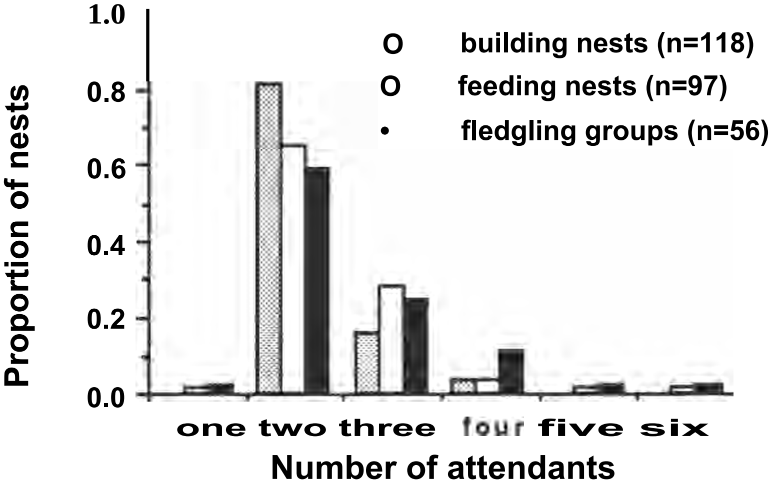


Figure 1. The proportion of feeding nests, building nests, and fledgling groups with 1-6 attendants (1986-1989).

The method by which bushtit nests acquired supernumeraries may be unique among cooperative breeders. Early in the breeding season or following a nest failure, single individuals or displaced pairs of birds contested over nests within the same flock. Because nests are costly structures, birds without nests may be willing to fight over an existing nest rather than building a new one. This competition resulted in either a successful ownership exchange or a compromise between the residents and the competitors in which both remained and attended the nest together. These multibird nests may have even been polygamous units: I observed situations in which some supernumeraries may have contributed genetically to clutches.

Proximate causes of variation

I found that bushtits in the Chiricahua Mountains exhibited spatial and temporal variation in social organization and incidence of nests with supernumeraries. For example, in 1987, 57% of nests had supernumeraries, while only 15% did so in 1989. Thus, in any given year, some nests had multiple attendents and some did not. These differences could be partially explained by facultative responses of birds without nests to characteristics of existing nests and their residents.

Compared to uncontested two-bird nests, nests with supernumeraries were in areas high in insect density (estimated from vegetation characteristics and density), low in predator (gray-breasted jay: *Aphelocoma mexicanus)* density, and were more likely to be attended initially by a yearling bird. These results support the hypothesis that birds target, for takeover or joining, nests that are more desirable or easier to contest. Unexpectedly, silver-leaf oak density *(Quercus hypoleucoides)* was positively correlated with contested status, but was also correlated with jay density, making it impossible to determine the relative importance of each on the contested status of a nest.

There was also support for the hypothesis that varying costs to potential helpers could determine which birds help and under what ecological conditions they help. In aviaries, food availability and helper condition modified response to playbacks of begging nestlings. Heavy, fasted birds moved more in response to the sounds of begging nestlings than did light, fasted birds, and this difference disappeared when both were sated. This suggests that food supply will have a greater effect on the helping behavior of individuals that are already physiologically stressed

Evolutionary scenario

Although they live in temporate climates, bushtits are poor thermoregulators (Chaplin 1982); they do not have physiological adaptations allowing them to cope with severe cold. I propose that this 'thermoregulatory constraint' has played a major role in the evolution of their complex social system by increasing the value of existing nests and limiting dispersal options (Figure 2). For example (Route A), the need to huddle to remain warm restricts bushtits to living in groups, making dispersal risky and resulting in philopatry and kin groups. Poor thermoregulation may also independently explain the presence of supernumeraries at nests (Route B): individuals may be willing to compromise and share a nest rather than risking exposure to the elements.

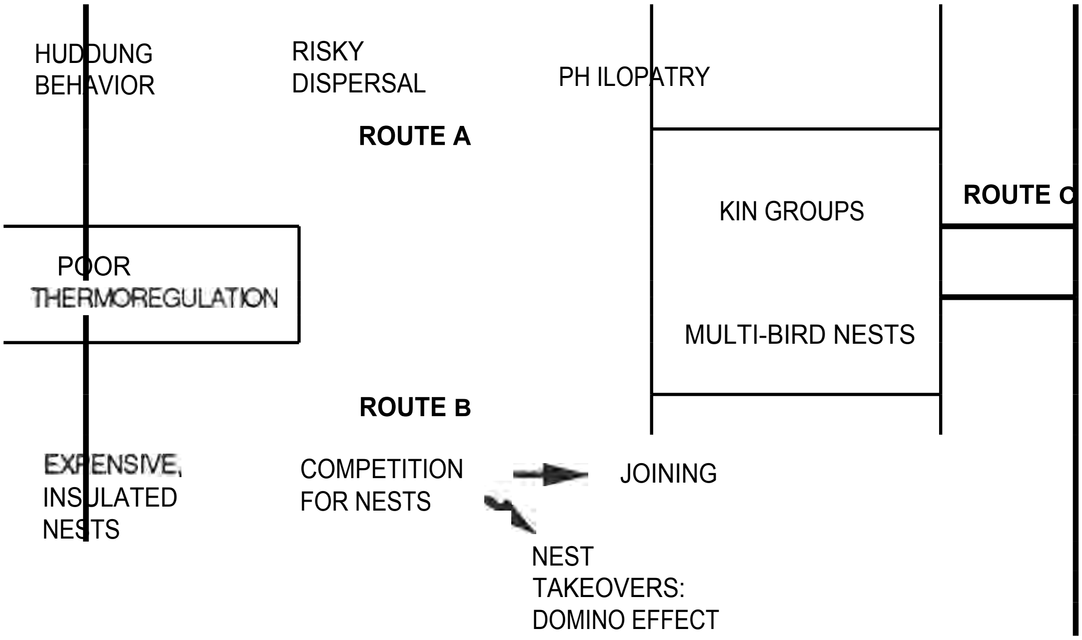


Figure 2. Diagram showing the proposed routes from the bushtit's thermoregulatory constraints to the social system. Huddling behavior results in philopatry and kin groups (Route A). Once built, heavily-insulated nests become a limited resource and competition for them leads to multibird nests (Route B). Route C is another route to multibird nests via kin selection once kin groups have formed.

Future research

The results of my study indicate several potential avenues for future research on bushtits, some of which I am currently pursuing: 1) The use of DNA fingerprinting to determine actual paternity and maternity at nests (currently in collaboration with Jeff Bruce at Hamilton University, Ontario, Canada). 2) The role of varying costs to potential joiners in the decision-making processes. 3) Geographic variation in ecology, such as predation and food supply, and its effect on the bushtit social structure. Using the characteristics I have found to be important to contested status of nests and the behavior of birds, I should beable to make predictions about when, and under what conditions, multibird nests become common.

In 1992, the bushtit population in the Chiricahua Mountains declined dramatically. The social structure changed in a predictable way, with fewer multibird nests and essentially no competition among individuals for existing nests. This kind of unusual event and its consequences underscores the importance of long-term studies to our perception of the complexity of social systems. Without, we can have only a limited understanding of the kinds of factors influencing variation in space and time and thus only a limited understanding of evolution and its consequences.

References

Brown, J. L. 1987. *Helping and Communal Breeding in Birds: Ecology and Evolution.* Princeton Univ. Press, Princeton, N.J.

Chaplin, S. B. 1982. The energetic significance if huddling behavior in Common Bushtits *(Psaltriparus minimus).* Auk 99: 424-430.

Darwin, C. 1859. *On the origin of species by means of natural selection. J.* Murray, London.

Emlen, S. T. and S. L. Vehrencamp. 1983. Cooperative breeding strategies among birds. In: *Perspectives in Ornithology.* Ed., A. H. Brush and G. A. Clark, Jr, pp. 93-120. Cambridge University Press, Cambridge.

Ervin, S. 1977. Bushtit helpers: accident or altruism? *Bird Behaviour* 1: 93-97.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. *J. Theor. Biol. 7: 1-*52.

Sloane, S. A. 1992. Supernumeraries at nests of bushtits *(Psaltriparus minimus):* incidence, origins, and proximate factors. Ph.D. dissertation, University of Michigan, Ann Arbor, MI.

Skutch, A. F. 1935. Helpers at the nest. *Auk* 52: 257-273.

Stacey, **P. B. and W. D. Koenig. 1990.** *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior.* Cambridge University Press, Cambridge, England.

* **Current address:** Sarah A. Sloane, Center for Evolutionary Ecology, T. H. Morgan School of Biological Sciences, University of Kentucky, Lexington, KY, 40506

METAPOPULATION STUDIES OF PIKAS

Andrew T. Smith
Department of Zoology, Arizona State University, Tempe, AZ 85287-1501

Introduction

Habitats are rarely continuous, and as a result their occupation by species populations is generally patchy. Increasingly these natural habitats, hence animal populations, are becoming fragmented and vulnerable as the result of human activities. We can apply the metapopulation concept (Gilpin and Hanski 1991) of interdependent patches of occupied and unoccupied habitat to describe the dynamics of these fragmented populations. The ultimate goal of this exercise is to understand these systems well enough to be able to predict their behavior and manage for their persistence.

The persistence of metapopulations is a function of the extinction rate of populations on individual patches and their probability of subsequent recolonization. A rich literature has outlined the factors that may influence the balance between extinction and colonization: size of patches, distance between patches, configuration of patches, species-specific demographic and genotypic patterns, and the ability of dispersers to move between patches (Gilpin and Hanski 1991; Ray et al. 1991; Smith and Peacock 1990).

Metapopulation dynamics of pikas

One of the most complete records regarding the behavior of a true metapopulations comes from my studies of pikas (Ochotona princeps), a small alpine lagomorph that occurs on islands of talus habitat at Bodie, California (Smith 1974a, 1974b, 1978, 1979, 1980, 1987). I have investigated the metapopulation dynamics of pikas since 1969, and in general I have found that the persistence of pikas on talus patches was determined by a dynamic equilibrium between extinction and recolonization. At any one time only a fraction of the talus patches was occupied, but there was great flux and overturn of populations on these patches between censuses.

In 1991 an unusual pattern emerged from the census of this population: almost all islands in the southern half of the study area were unoccupied, rather than the normal "mix" of occupied and unoccupied islands. Evidently in this region a global correlated extinction occurred that caused the near collapse of the pikas throughout the area. Such events can occur when the proportion of occupied patches, thus the sources of colonists to nearby vacant patches, falls below some critical threshold level. The observation of correlated extinctions of pika populations at Bodie is the first demonstration of this theoretical possibility.

Conservation take-home lessons

In all metapopulation systems there is a likelihood that populations that are viewed as stable and in equilibrium can collapse due to aspects of correlated extinctions and the concomitant reduction in recolonization rates of vacant patches. Thus when we monitor and/or manage species populations that are fragmented we should incorporate the possibility of metapopulation collapse for we may be at risk of losing species that previously had not been considered threatened. Many forms of biota in the Chiricahua Mountains are fragmented or distributed patchily, thus great care must be taken to ensure that the metapopulation concept, hence the possibility of local collapse of a population, is taken into consideration in aspects of their monitoring and management.

Literature cited

Gilpin, M. and I. Hanski (editors). 1991. Metapopulation dynamics: empirical and theoretical investigations. Academic Press.

Ray, C. L., M. E. Gilpin and A. T. Smith. 1991. The effect of conspecific attraction on metapopulation dynamics. Biological Journal of the Linnean Society 42:123-134.

Smith, A. T. 1974a. The distribution and dispersal of pikas: consequences of insular population structure. Ecology 55:1112-1119.

Smith, A. T. 1974b. The distribution and dispersal of pikas: influences of behavior and climate. Ecology 55:1368-1376.

Smith, A. T. 1978. Comparative demography of pikas (Ochotona): effect of spatial and temporal age-specific mortality. Ecology 59:133-139.

Smith, A. T. 1979. Equilibrial population structure of pikas. Murrelet 60:29-31.

Smith, A. T. 1980. Temporal changes in insular populations of the pika (Ochotona princeps). Ecology 60:8-13.

Smith, A. T. 1987. Population structure of pikas: dispersal versus philopatry. Pp. 128-142. In: Mammalian dispersal patterns: the effects of social structure on population genetics. B. D. Chepko-Sade and Z. T. Halpin, editors. University of Chicago Press.

Smith, A. T. and M. M. Peacock. 1990. Conspecific attraction and the determination of metapopulation colonization rates. Conservation Biology 4:320-323.

REINTRODUCTION OF THE THICK-BILLED PARROT IN THE CHIRICAHUA MOUNTAINS

Noel F.R. Snyder
Wildlife Preservation Trust International,
P.O. Box 426, Portal, Arizona

Terry B. Johnson
Arizona Game and Fish Department
2221 West Greenway Road, Phoenix, Arizona 85023-4312

Introduction

The thick-billed parrot (Rhynchopsitta pachyrhyncha) is one of only two species of parrots native to the continental United States, and was formerly found with some regularity in southeastern Arizona and southwestern New Mexico, especially in the Chiricahua Mountains (Wetmore 1935). However, sightings became increasingly scarce during the 1920's and 1930's, and the last well-documented historical report for the population in the United States was in 1938 in Chiricahua National Monument (Monson and Phillips 1981). At present, the thick-billed parrot is considered endangered in its remaining wild population in the Sierra Madre Occidental of Mexico (Collar and Juniper 1992). Although no comprehensive censuses of the Mexican population have been conducted, the species is apparently still widely distributed and found in some thousands of individuals in Mexico.

The thick-billed parrot disappeared from the United States before any intensive studies were conducted of its biology. No nests were documented in the states prior to its disappearance, but this may have been less an indication of a failure of the species to breed here than it was a reflection of a lack of any comprehensive efforts to find nests. Almost all our information on the species in the United States came from incidental observations of ranchers, miners, and lumberman; not from trained ornithologists. While most authors have concluded that the species was not a permanent resident north of the border, and it is clear that many records pertain to incursions of birds from Mexico, it also appears from interview data that there may have been an established population in the Chiricahuas at one time (Snyder and Wallace 1987). Wetmore (1931) reported historical data suggesting the species once occurred as far north as central Arizona. In Mexico, the species has been the subject of only one important study (Lanning and Shiflett 1981, 1983).

The thick-billed parrot feeds mainly on pine cones, although it also takes acorns to a limited extent. At the latitude of southern Arizona and northern Mexico, it generally centers its activities at elevations of about 2,000 to 3,000 m elevation, commonly nesting in old flicker (Colaptes auratus) cavities in snags of ponderosa pine (Pinus ponderosa). The species is decidedly social at all times of year and is partially nomadic in response to local fluctuations in its primary food supplies.

Causes of the disappearance of the Thick-billed Parrot from the United States are uncertain. There was some substantial cutting of the pine forests associated with early mining activities, but it appears that many of the steeper and more inaccessible wooded canyons were left untouched by such activities. Thus, the extent to which habitat destruction contributed to the decline is quite speculative. Less speculative were the impacts of shooting. Almost all of the early published reports of thick-bills in the United States mention substantial shooting pressures (e.g., Lusk 1900, Smith 1907, Vorhies 1934, Wetmore 1935), and in interviews of oldtime residents of the Chiricahuas we have heard repeated tales of widespread and relentless killing for food. Like many other parrots, thick-billed parrots are highly vulnerable to shooting because of their large size, their extraordinarily loud vocalizations, their highly social habits, and their general tolerance for close approach by humans. We consider shooting to be the most probable main cause of extirpation.

If shooting was indeed the major problem, then prospects for reestablishing the species in southern Arizona would appear to be good, because subsistence hunting has largely disappeared from the region. Moreover, the mountain forests of southern Arizona are now largely free of timber cutting.

Reintroduction Attempts

In the mid-1980's large numbers of thick-billed parrots began to turn up in captivity in the United States, largely as a result of a great expansion in illegal capture of the species in Mexico and smuggling of birds across the border. Some of these birds were confiscated in enforcement activities of the U.S. Fish and Wildlife Service, and the availability of these birds led to a proposal to initiate a reintroduction program in Arizona in mid-1986. The original program was organized with the Arizona Game and Fish Department as lead agency and with cooperative contributions by the U.S. Forest Service and the U.S. Fish and Wildlife Service. In subsequent years many private organizations and individuals have also joined the effort, especially the Wildlife Preservation Trust International, the World Bird Sanctuary in Missouri, the Avicultural and Breeding Research Center in Florida, and a diversity of United States zoos. In addition, the Southwestern Research Station in Cave Creek Canyon has provided considerable manpower and logistic support through its volunteer program. Veterinary support has been contributed by James Koschmann and David Graham of Texas.

A number of pilot releases of thick-billed parrots have now been conducted in the Chiricahua Mountains. The Chiricahuas were chosen as the most favorable release area mainly because most historical reports of the species have come from these mountains, but also because the Chiricahuas are the largest of the "sky islands" and have the greatest area of pine forests. Releases have involved birds of three sorts: (1) birds taken from the wild as free-flying individuals in Mexico, (2) birds hand-reared in captivity, and (3) birds parent-reared in captivity. Not surprisingly, the most successful experiments have involved wild-caught birds returned to the wild.

The first releases in 1986 were conducted with wild-caught birds and resulted in a wild flock of about a dozen birds which established residence in Cave Creek Canyon during the winter months and migrated annually to the headwaters of Tonto Creek in central Arizona during the summer, a distance of some 250 miles. After initially heavy mortality this flock showed good annual survival, and one pair was documented breeding successfully in the wild in 1988. Breeding was again recorded in 1989, in two pairs, but was unsuccessful, primarily because of a drought-related failure of the food supply late in the year. Mortality was again relatively heavy in 1989 and 1990, probably due both to poor food supplies and to low numbers of birds in the flock, which left the birds relatively vulnerable to predation. The flock became nomadic in late 1989 and we were unable to track the remaining birds beyond the end of the year because of failure of the last active radio transmitters in the flock. The last sighting of birds apparently from this flock (a single pair) was recorded in late 1990.

Results with hand-reared captives were much less encouraging. A release of a half-dozen such birds in late 1987 indicated major behavioral deficits in flocking behavior, predator avoidance, and feeding behavior, despite intensive conditioning of birds prior to release. These birds were all recaptured shortly after release, when it became apparent that they had no real potential for survival in the wild.

Results with parent-reared captive-born birds have been better, but indicate that these birds are also at a substantial disadvantage compared to wild-caught birds. A mixed release of wild-caught and parent-reared captive-born birds was conducted in late 1991. Several of the captive-reared birds did integrate with wild-caught birds and did demonstrate rapid improvement in feeding and social behaviors after release, but mortality of birds was heavy due in part to a food supply that was not optimal and to especially heavy goshawk (*Accipiter gentilis*) predation that resulted from a need to subsidize the released birds in a fixed location. Survivors from this release were brought back into captivity in January 1992 because of the poor conditions. The captive-reared birds that did best in this release were all very young birds and were mostly birds that had had considerable experience in a very large cage prior to release.

Thus results overall indicate that wild-caught birds are by far the most favorable birds to use in reintroduction efforts. It may also be possible to get some captive-reared birds to survive in the wild, but perhaps only if they are given an opportunity to join a preexisting wild flock, and only if they are parent-reared in captivity. Hand-reared birds appear to have no appreciable value for reestablishment efforts in wild environments.

Unfortunately, very few wild-caught birds have been available for release efforts in recent years, so success in reestablishment now appears to depend primarily on getting at least a small wild-caught flock reestablished in the wild and bolstering this flock with substantial numbers of parent-reared, captive-born birds. Future experiments will further test the importance of youth and large-cage experience for survival of captive-reared birds.

The principal resistance factors to reestablishing the species in the wild appear to be goshawk predation and periodic failures in food supplies. Presumably the abilities of a released flock to handle both these factors may be enhanced as a function of flock size and breadth of geographic distribution. While it is still early to say that the species may be successfully reestablished in Arizona, we are generally encouraged by the results so far, and feel that the principal obstacle to success remains the obtaining of sufficient numbers of high quality birds for release. Experiments so far have established that at least some individuals appear to find Arizona a congenial home and are willing to breed in this region. Although there were early fears that many released birds would simply home to Mexico, this has not been a major tendency.

Literature Cited

Collar, N.J., and A.T. Juniper. 1992. Dimensions and causes of the parrot conservation crisis. Pp 1-24 in New World parrots in crisis, solutions from conservation biology (S.R. Beissinger and N.F.R. Snyder, eds.), Smithsonian Institution Press, Washington, D.C.

Lanning, D.V., and J.T. Shiflett. 1981. Status and nesting ecology of the thick-billed parrot (*Rhynchopsitta* pachyrhyncha). Pp 393-401 in Conservation of New World parrots. (R.F. Pasquier, ed.), Smithsonian Institution Press, Washington, D.C.

Lanning, D.V., and J.T. Shiflett. 1983. Nesting ecology of thick-billed parrots. Condor 85:66-73.

Lusk, R.D. 1900. Parrots in the United States. Condor .2:129.

Monson, G., and A.R. Phillips. 1981. Annotated checklist of the birds of Arizona, 2nd ed. University of Arizona Press, Tucson.

Smith, A.P. 1907. The thick-billed parrot in Arizona. Condor 9:104.

Snyder, N.F.R., and M.P. Wallace. 1987. Reintroduction of the thick-billed parrot in Arizona. Pp 360-384 in Proceedings 1987 Jean Delacour/IFCB Symposium on Breeding Birds in Captivity.

Vorhies, C.T. 1934. Arizona records of the thick-billed parrot. Condor 36:180-181.

Wetmore, A. 1931. Early record of birds in Arizona and New Mexico. Condor 33:35.

Wetmore, A. 1935. The thick-billed parrot in southern Arizona. Condor 37:18-21.

BIOLOGY OF NORTH AMERICAN ACCIPITERS IN THE CHIRICAHUA MOUNTAINS

Noel F.R. Snyder
Wildlife Preservation Trust International
P.O. Box 426, Portal, AZ 85632

Helen A. Snyder
P.O. Box 426, Portal, AZ 85632

Introduction

Three species of hawks of the genus Accipiter occur in North America, and all three occur sympatrically in the Chiricahua Mountains. The sharp-shinned hawk (Accipiter striatus) is the smallest of the three and possesses the greatest sexual size dimorphism of any North American raptor, with females weighing nearly twice as much as males. Cooper's hawk (Accipiter cooperii) is somewhat larger and also exhibits quite strong sexual size dimorphism. The goshawk (Accipiter gentilis) is the largest of the three and exhibits the least amount of sexual size dimorphism. All three species feed quite heavily on other birds, with the sharp-shinned hawk taking birds almost exclusively; the Cooper's hawk taking mostly birds, but some lizards and chipmunks; and the goshawk taking many squirrels and rabbits in addition to large birds, such as jays and pigeons. The similarities in diet and general habitat preferences of these three species and their close spatial distribution in the Chiricahuas makes this region an ideal place to study their comparative behavior and ecology.

General Behavior and Abundance

The three accipiters are all birds of forest and forest edge habitats. Adapting them to such habitats are relatively short wings, long legs, and long tails. They are all highly maneuverable species capable of rapid accelerations and tight turns in an air space cluttered with branches and other obstacles.

Historically, Cooper's hawk was the most abundant of the three species in the Chiricahuas, with nesting pairs spaced about a mile apart in most wooded drainage systems. When we studied the three species in the late 1960's and early 1970's, Cooper's hawks appeared to be occurring in near-saturation densities and exhibited good overall nesting success in spite of considerable contamination with DDE. Nesting populations of this species were exceedingly stable from year to year. Goshawks and sharp-shinned hawks occurred in much lower numbers. They also appeared to be relatively stable in population sizes, but this was difficult to judge rigorously.

When we returned to the Chiricahuas in 1986, however, we found the abundances of the accipiter species to be changing dramatically. In particular, Cooper's hawks had declined greatly, with less than half as many pairs in our survey areas. This decline has worsened progressively in more recent years. Sharp-shinned hawks, in contrast, appeared to be more abundant than they were twenty years ago, though they were still a relatively uncommon species. Recent goshawk trends are more uncertain, and there is a need for a comprehensive survey of goshawk territories to establish the present status of this species. We suspect that numbers of nesting goshawks have declined somewhat in recent years, but this needs verification. Causes of the major decline in Cooper's hawks are not known. Nesting success of the pairs that still exist appears to be within the normal range, and prey supplies and habitat quality appear to be similar to what they were 20 years ago. Our main concerns center on potential mortality factors on the wintering grounds of this species in Mexico.

Diet and Spacing

In the late 1960's and early 1970's we conducted intensive studies of the behavior and ecology of all three species from blinds set up on nests. These observations allowed us to obtain large amounts of information on diet of the three species and to determine the degree of overlap in feeding habits between species and between sexes within species. There was considerable overlap between the diets of Cooper's hawks and goshawks, with both species taking large numbers of jays (Aphelocoma ultramarina and Cyanocitta stelleri) and band-tailed pigeons (Columba fasciata). However, we never documented goshawks taking lizards or chipmunks, though these prey types were abundant in the foraging ranges of Goshawk pairs. Chipmunks (Eutamias dorsalis) and lizards (mostly Sceloperus sp) formed about 45% of Cooper's Hawks diet. There was also considerable overlap between diets of Cooper's hawks and sharp-shinned hawks in that both species frequently took medium-sized birds, such as black-headed grosbeaks (Pheucticus melanocephalus) and robins (Turdus migratorius). However, lizards were very infrequent in the diet of sharp-shinned hawks, and we never observed them taking mammals. Many of the birds they captured were also below the size normally taken by Cooper's hawks.

With the fair degree of overlap in prey exhibited between goshawks and Cooper's hawks and between Cooper's hawks and sharp-shinned hawks (but not between goshawks and sharp-shinned hawks), we were curious to examine the spatial distribution of nests among the three species. Here we found a most interesting pattern. Goshawks and Cooper's hawks spaced their nests pretty much as if they were all one species -- that is, with distances of about a mile between adjacent nests. Similarly, Cooper's hawks and sharp-shinned hawks usually spaced their nests about a mile from one another. In contrast, we found a number of cases of sharp-shinned hawks nesting immediately adjacent to goshawks -- close enough that one could hear the vocalizations of nestlings of one species while standing at the nest of the other. The near absence of prey overlap between these two species, suggested a near absence of food competition and the close spacing of nests of these species seemed reasonable on these grounds. In fact, we suspected that with the near saturation densities of Cooper's hawks in the region that goshawks might be performing a most valuable function for sharp-shinned hawks by creating Cooper's hawk-free zones in which the sharpshins could nest. About the only places we found sharpshins nesting were either immediately adjacent to

Goshawks or in Cooper's hawk territories that were vacant in particular years.

Nevertheless, the spacing of nests of the three species may also reflect other factors than food competition. The larger species represent direct threats of predation on the smaller, and the smaller species may space themselves maximally from the larger to reduce such threats. However, while this argument appears relevant to the spacing between Cooper's hawks and goshawks, and between Cooper's hawks and sharp-shinned hawks, it does not at first sight fit well with the frequent close spacing of sharp-shinned hawk and goshawk nests. Our detailed observations at nests of these two species provided a potential explanation for the apparent contradiction. Sharp-shinned hawks in this region chose such dense microhabitats for nesting that their nests may have been largely inaccessible to goshawks even though they often nested very close to them. In fact, we commonly observed sharp-shinned hawks nesting in such dense tangles that they were obliged to bang their wings quite brutally against branches in flying to and from their nests. It appeared that their nests were generally in locations that were very difficult for the goshawks to penetrate. As direct evidence of this, we once observed a female goshawk attempting to fight through the dense branches of a fir to gain access to fledgling sharpshins standing on their nest. The goshawk was not able to force its way to the nest itself and all sharpshins scattered to safety. All of the sharp-shinned hawk pairs we found nesting immediately adjacent to goshawks were successful in fledging their young.

Other Studies

While there was considerable overlap in the prey taken by adjacent size pairs of accipiters, we nevertheless found significant prey size differences for different sexes within species in both sharp-shinned hawks and Cooper's hawks. For example, in the sharp-shinned hawk, males usually took prey that were junco-sized or smaller, while females often took grosbeaks and robins. In Cooper's hawk, males concentrated on chipmunks, lizards, and grosbeak- to robin-sized birds, while most jays and pigeons were taken by females. The sexual differences in diet were sufficiently strong in these two species to suggest significant advantages in increasing food availability during the breeding season, and it appeared this effect might be especially important in the late breeding season -- July and August -- when we saw most food-related mortality of nestlings and fledglings (Snyder and Wiley 1976).

Other studies we conducted on these species included detailed descriptive documentation of nesting behavior through the nesting cycle, especially with respect to division of labor between sexes (Snyder and Snyder 1979, 1992); effects of pesticides on the biology of these birds (Snyder et al. 1973); experimental studies of the effects of brood size on foraging rates (Snyder and Snyder 1973); banding studies (Snyder and Snyder 1974a); and experimental studies of the function of variations in eye coloration found in these birds (Snyder and Snyder 1974b). Within Cooper's hawk we were able to document a substantial cline in diet with altitude, and along with this cline, a parallel cline in DDE contamination. Pairs nesting at relatively low elevations tended to take relatively large numbers of chipmunks and lizards in their diet, while pairs at high elevations tended to feed mostly on other birds. Not surprisingly, the pairs at high elevation tended to be the most contaminated with DDE. In addition, we were able to demonstrate that the timing of egglaying in Cooper's hawk was related to altitude, with pairs at high altitude breeding later than pairs lower down. The wide altitudinal range present within the Chiricahuas gives an excellent opportunity to examine the effects of various environmental features on the biology of these birds within a very small area.

Literature Cited

Snyder, H.A., and N.F.R. Snyder. 1974a. Increased mortality of Cooper's hawks accustomed to man. Condor 76:215-216.

Snyder, N.F.R., and H.A. Snyder. 1973. Experimental study of feeding rates of nesting Cooper's Hawks. Condor 75:461-463.

Snyder, N.F.R., and H.A. Snyder. 1974b. Function of eye coloration in North American accipiters. Condor 76:219-222.

Snyder, N., and H. Snyder. 1979. Biology of North American accipiters in Arizona and New Mexico. National Geographic Society Research Reports, 1970 projects, pp 487-491.

Snyder, N., and H. Snyder. 1992. Birds of prey, natural history and conservation of North American raptors. Voyageur Press, Stillwater, Minnesota.

Snyder, N.F.R., H.A. Snyder, J.L. Lincer, and R.T. Reynolds. 1973. Organochlorines, heavy metals, and the biology of North American accipiters. BioScience 23:300-305.

Snyder, N.F.R., and J.W. Wiley. 1976. Sexual size dimorphism in hawks and owls of North America. Ornithological Monographs No. 20.

SEASONAL MOVEMENTS OF WHITE-TAILED DEER *ODOCOILEUS VIRGINIANUS COUESI* IN THE CAVE CREEK BASIN OF THE CHIRICAHUA MOUNTAINS, COCHISE COUNTY, ARIZONA

Joseph M. Welch
Southwestern Field Biologists
Tucson, Arizona

INTRODUCTION

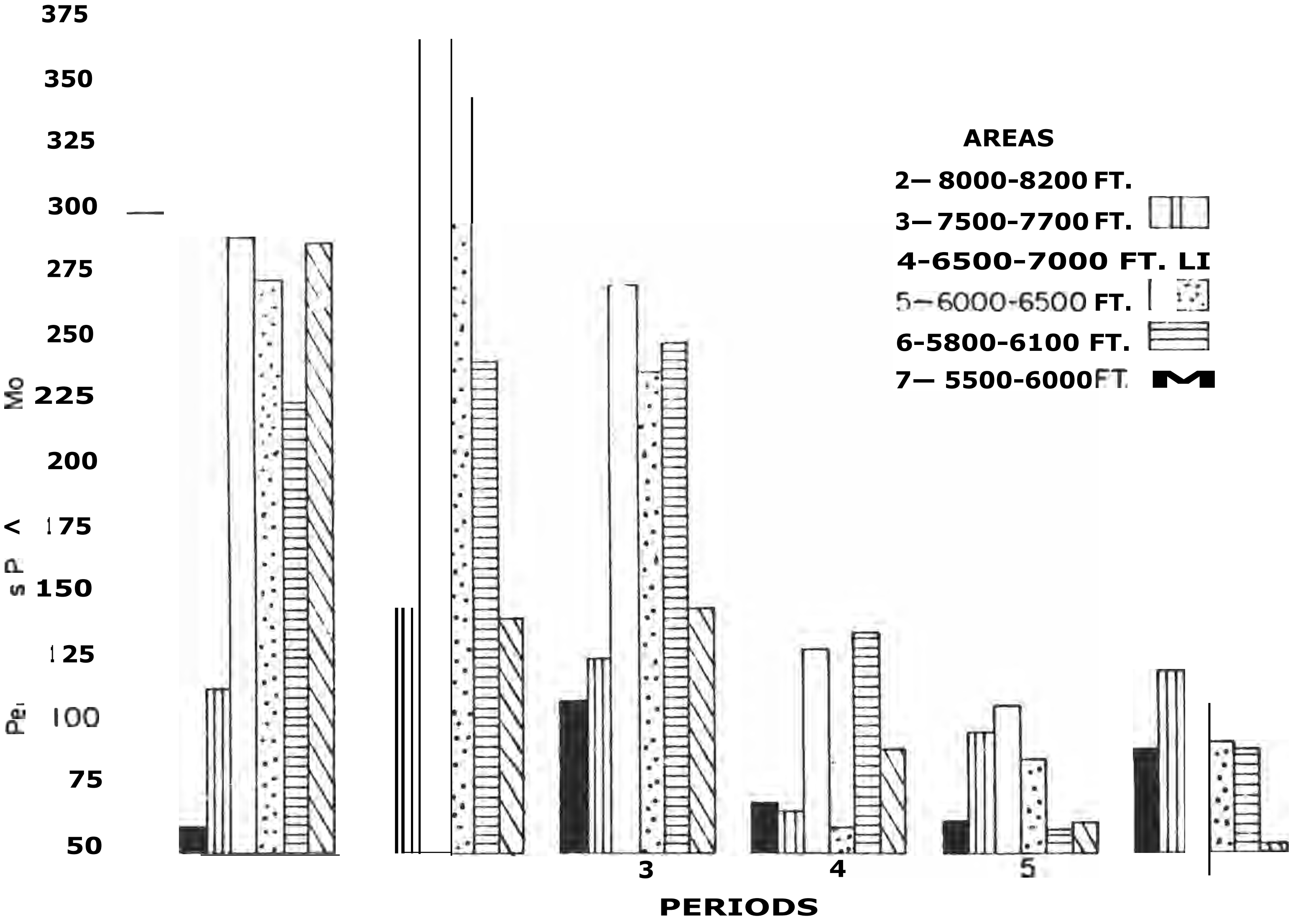
Seasonal movements of the Coues white-tailed deer were studied in the Chiricahua Mountains in 1958 and 1959. Methods used to study movements were: (1) periodic pellet-group counts on circular plots in seven study areas ranging from 5,500 to 9,500 feet in elevation ; (2) monthly roadside track counts in the major elevational levels; and (3) sight observations on deer in all elevations throughout the year.

The Coues white-tailed deer did not exhibit a true seasonal migration. Movements were influenced by seasonal availability of food, water, cover, and breeding activity. Maximum movements occurred during the rut, early winter, spring and early summer. The close juxtaposition of varied habitats and exposures resulted in short movement distances.

Statistical analysis of pellet-group counts indicated the data followed a Poisson distribution rather than a normal one. This indicates that pellet-group count data is not amenable to analysis of variance and other forms of statistical analysis. In this study, pellet-counts decreased when deer switched to feeding on succulents. Deer density varied significantly by elevation and vegetative type with the highest density occurring in the 6,000-7,000 foot elevations.

Six pellet-group counts and ten roadside track counts were obtained during the study. Pellet-group counts were recorded every 50 to 60 days, while track counts were obtained on three successive days each month. The study period was divided into six segments as follows: two winter, one spring, two summer, and one fall surveys.

The time interval between pellet-group counts was not equal for each period sampled. Counts are presented as pellet-groups per acre per month to make direct comparisons possible, see graph for comparisons by study areas and elevations. Deer densities were calculated from pellet-group counts,using the daily defecation rate of 13.0 pellet-groups per deer per day. These figures reflect varying densities of deer at different elevations resulting from seasonal movements.



COMPARISON OF PELLET GROUPS PER ACRE, PER MONTH BY PERIOD AND AREA.

Elevation Range	Av. No. Deer Per Sq. Mile	Variance ofDeer Per Sq. Mile
8,000+	12	7-17
7,000-8,000	18	7-26
6,000-7,000	37	17-71
5,000-6,000	26	13-43

RESULTS

Observations of deer during the study yielded the following sex and age ratios: average bucks per 100 does was 64, and ranged from 31 - 153. Correspondingly, fawns per 100 does averaged 57, and ranged from 18 - 94.

Observations of deer, roadside track counts and pellet-group counts were all used in determining seasonal deer movements. My obserations of deer for extended periods along with pellet-group counts on transect plots indicated that deer defecation rates varied throughout the year. Defecation rates increased greatly during the rut. That fact along with deer banding into herds by bucks, resulted in a skewed distribution of pellet-group count data collected at that time. Seasonal changes in diets, sex and age of the animal affected defecation rates. Consequently deer movements based solely from pellet-group counts maybe misleading, but pellet-group counts in conjunction with observations of deer and roadside track counts provided reliable seasonal deer movement data.

CONCLUSIONS

This study documented seasonal movements of the Coues white-tailed deer. Of equal or greater significance are the problems associated with the use of pellet-group counts in determining Coues white-tailed deer densities. Deer densities computed from pellet-counts were skewed higher than the number of deer actually using the transect areas. Deer numbers at that time were at a record high in the Chiricahua Mountains. Further study is needed to increase the reliability of pellet-group counts before too much confidence can be placed on using the defecation rate of 13.0 pellet-groups per deer per day as an indicator of population density.

LITERATURE CITED

Welch, J.M. 1960. A Study Of Seasonal Movements Of White-tailed Deer In The Cave Creek Basin Of The Chiricahua Mountains. M.S. Thesis, Univ.

THE EARED TROGON IN ARIZONA:
BEHAVIOR, ECOLOGY, AND MANAGEMENT OF THE "NORTHERN QUETZAL"

Sheri L. Williamson
The Nature Conservancy, Ramsey Canyon Preserve
27 Ramsey Canyon Road
Hereford, AZ 85615

Introduction

The Eared Trogon, *Euptilotis neoxenus,* is endemic to the pine-oak forests of the Sierra Madre Occidental of Mexico and is recorded from the northern edge of the range within 160 km of the Arizona-Mexico border (Marshall 1957). This close relative of the Resplendent Quetzal *(Pharomachrus mocinno)* was added to the avifauna of Arizona in late 1977, when individuals were sighted in Cave Creek Canyon in the Chiricahua Mountains and Ramsey Canyon in the Huachuca Mountains. Despite sightings in the Chiricahuas virtually every fall since 1977 (Davis and Russell 1990) and predictions that the species would eventually be found nesting in the United States (Zimmerman 1978), there was no conclusive evidence of nesting until October 1991, when a pair of Eared Trogons was discovered feeding young in a tree cavity in upper Ramsey Canyon in the Huachuca Mountains.

My involvement with Eared Trogons began on 5 August 1991, when a male and female were discovered in the Coronado National Forest Miller Peak Wilderness within 1 km of the boundary of The Nature Conservancy's Ramsey Canyon Preserve. The sighting in Ramsey Canyon was not altogether surprising as it followed weeks of sporadic sightings of this species along the South Fork Trail in Cave Creek Canyon beginning on 9 June. News of the Ramsey Canyon sighting reached the birding community within days of the discovery, and the presence of Eared Trogons in upper Ramsey Canyon was soon announced on the North American Rare Bird Alert. By early November Eared Trogons had been reported from five locations in southeastern Arizona, but only the South Fork and Ramsey Canyon birds were seen by large numbers of birders.

The results of the announcement were immediately apparent to preserve personnel. Between 13 and 18 August, at least 138 people who came to Ramsey Canyon Preserve were turned away after the preserve reached capacity, and many who telephoned the preserve for information were encouraged to avoid the preserve in favor of National Forest trailheads at Brown and Carr canyons. Visitation at the preserve from 13 to 31 August was 45% higher than the same period in 1990, and use of the Hamburg Trail, which provides access through the preserve to the Miller Peak Wilderness, more than doubled over the same period, from 229 users in 1990 to 489 in 1991. Use statistics for the two nearby National Forest trailheads are not available, but these areas normally attract only a fraction of the visitation of Ramsey Canyon Preserve and so may have experienced even more dramatic increases in use.

Informal records of staff, visitor, and volunteer reports of the birds were kept in the wildlife sightings log at Ramsey Canyon Preserve beginning on 5 August. Many but not all of the entries note the number, sex, location, and behavior of the bird or birds observed. Preserve staff also received reports of birder behavior, including shouting, running, loud and continuous playing of taped trogon calls, and off-trail pursuit of the birds (including at least one intrusion on a documented den site for the rare ridge-nosed rattlesnake, *Crotalus willardi).*

Birder success was far from 100%, and the proportion of successful parties appeared to decline as larger numbers of people entered the area. As activity increased in the upper canyon, sightings of the trogons began coming in from further upstream, until the pair seemed to settle into an area in lower Pat Scott Canyon more than 2 km from the site where they were first seen. Sightings from areas downstream continued, but the proportion of reports from the original sighting area declined. Visitor activity declined somewhat after the first week, and dropped off sharply following Labor Day.

On 9 September Tom Wood and I visited the area in response to reports of possible nesting behavior and observed a trogon of unknown sex entering a woodpecker nest cavity in a dead conifer at 2100 m in lower Pat Scott Canyon. We observed that the bird entered the cavity whenever it began to rain and emerged when the rain stopped; this fact plus the time of year convinced us that we had observed shelter-seeking behavior, not nesting. On 10 October a group of birders videotaped a female entering a cavity in a dead big-toothed maple (A[illegible]) approximately 1.3 km downstream from the site of the first cavity and easily visible from the Hamburg Trail; a member of the same group returned on 12 October and observed a male carrying a caterpillar into the same cavity, indicating the presence of young. On 14 October I watched the tree from 1130 to 1530, observed 6 feeding visits by the adults, and was able to confirm the presence of two chicks by tapping the tree and listening to the nestlings' hissing begging calls.

With nesting confirmed, I initiated a volunteer monitoring program with the assistance of the Tucson and Huachuca Audubon Societies. Volunteers were present at the site every day to record observations of both trogon and birder behavior, and were also provided with viewing guidelines intended to prevent or minimize disruption of the birds' behavior by both observers and monitors. More than 60 hours of observations at the nest site provided a wealth of data on the birds' behavior at the nest, including their response to human presence and behavior.

The male was the more vocal member of the pair, giving the "squeal-chuck" call and cackling flight call more often and for longer periods than the female. He was also more cautious when approaching the nest, particularly when there was conspicuous human activity along the trail. On one occasion the male arrived at the nest with food, aborted three attempts to enter the nest, and flew around the nest area in an agitated manner over a period of 14 minutes but did not enter the nest to feed the young until an observer removed and concealed his white shirt and cap. In contrast, the female usually flew quickly to the hole and entered immediately, but would typically pause at the nest entrance for a few moments before departing.

On the afternoon of 26 October the first storm of the winter reached the Huachucas. Overnight temperatures at the preserve weather station (elevation 1720 m) dropped to -3° C., and temperatures at the nest site were likely 3° colder. The last recorded nest visit by an adult trogon was reported the next morning. On 28 October the pair were found together at midmorning and early afternoon in a grove of fruiting Arizona madrone trees *(Arbutus arizonica)* just inside the upstream boundary of Ramsey Canyon Preserve. On 30 October volunteers from the Bisbee Fire Department climbed the nest tree and recovered the bodies of the two young trogons.

One of the chicks died of unknown causes several days before the other; due to the poor condition of the carcass its age and cause of death could not be determined. Its nestmate appeared to have survived until the storm, then succumbed to hypothermia. Its well-preserved body was well-fleshed, full-bellied, and partly covered in a coat of black and yellow down. Based on documented developmental stages in Resplendent and Golden-headed quetzals, this chick was between 18 and 21 days old and 7 to 12 days from fledging at the time of death.

The adult trogons apparently stayed in the area throughout the winter, remaining mostly in the restricted area of Ramsey Canyon Preserve, though there were several sightings in nearby Scheelite Canyon. Sightings became more regular in early February, and word once again spread in the birding community. February visitation at the preserve increased by 5% and use of the Hamburg Trail increased by 20% over February 1991. Both male and female trogons were present on the preserve the first week of March and made sporadic appearances along the Hamburg Trail. On 15 March 1992, 30 people went up the Hamburg Trail between 0800 and 0915, all looking for the elusive trogons.

Conclusions and Future Research

Based on information gained from my own and others' observations of Eared Trogons in Ramsey and Cave Creek canyons, reports of field observations of Eared Trogons in Mexico (R. Taylor, pers. comm.), and personal field observations of seven species of typical trogons (genus *Trogon)* and the Resplendent Quetzal, I have drawn some tentative conclusions about the behavior and reproductive cycle of this species:

1. Its normal nesting season coincides with the summer rains, commencing in late July and early August.

2. The young develop at approximately the same rate as quetzal chicks, have a nestling period of approximately four weeks, and normally leave the nest by the end of September.

3. It is essentially non-migratory and may remain in or near its nesting territory during the winter.

4. It is strikingly less tolerant of human activity than typical trogons such as the Elegant Trogon *(Trogon elegans)*.

The 1977 sightings of this species attracted hundreds of birders from throughout the U.S., and this intense activity caused concern for the future of the Eared Trogon as a breeding species in Arizona (Zimmerman 1978). Given their observed sensitivity to human activity and long nestling period, Eared Trogons may be much more susceptible to human-caused nesting failure than Elegant Trogons. Taylor (1979) has observed that interference from birders attempting to photograph nests is a significant cause of nest abandonment by Elegant Trogons in Cave Creek Canyon. While the late initiation of nesting is the superficial cause of this nest failure, the birds' movements in the canyon during periods of greater and lesser human activity suggest that birding pressure was a factor in delaying nesting.

Informal observations of birder behavior in Ramsey Canyon suggest that, despite their generally high level of environmental awareness and concern, birders in the field often act in ways which may be detrimental to birds and/or their habitat. This agrees with a study of birder behavior conducted at Point Pelee National Park, a birding "hotspot" in southern Canada (Butler and Fenton 1986). Given the increasing numbers of birders coming to southeastern Arizona each year, the growth of competitive birding, and the efficiency of the birding information network, the scenes in Ramsey Canyon and South Fork in 1991 are likely to be repeated with even greater intensity following each appearance of a "rarity."

Birding has a major economic impact on southeastern Arizona, and has been a significant factor in the success of land conservation in this part of the state. This positive economic impact is created largely by the presence of dependable "rarities" such as Elegant Trogons and Red-faced Warblers, and is enhanced by the serendipitous appearance of species such as Eared Trogons. If Eared Trogons are to become established in areas of southeastern Arizona with reasonable access to birders, and if human impact on the birds and the sensitive natural areas they frequent is to be maintained at reasonable levels for the health of the entire ecosystem, we must learn a great deal more about the behavior of both the trogons and their human admirers, and we must apply what we learn to the management of highly popular birding areas such as South Fork and Ramsey Canyon.

Literature Cited

Butler, J. R. and G. D. Fenton. 1986. Bird watchers of Point Pelee National Park, Canada: Their characteristics and activities, with special consideration to their social and resource impacts. First National Symposium on Social Science in Resource Management, Oregon State University, Corvallis, Oregon. [Cited in Dunne, P. 1992. *The Feather Quest.* Dutton/Penguin, New York, New York.]

Davis, W. A. and S. M. Russell. 1990. *Birds In Southeastern Arizona.* Tucson Audubon Society, Tucson, Arizona.

Marshall, J. T. 1957. Birds of Pine-Oak Woodland in Southern Arizona and Adjacent Mexico. *Pacific Coast Avifauna* 32: 82-83.

Taylor, R. 1979. Progress Report: The Coppery-tailed Trogon in Arizona, 1979. Unpublished.

Zimmerman, D. A. 1978. Eared Trogon — immigrant or visitor? *American Birds* 32: 135-139.

OTHER ECOLOGICAL APPLICATIONS
IN THE CHIRICAHUA MOUNTAINS

THE BIOPOLITICS OF CAVE CREEK: A PRELIMINARY INVESTIGATION

Mari N. Jensen
School of Renewable Natural Resources, University of Arizona,
Tucson, AZ 85721

Introduction

Within the last two decades, the doctrine of multiple use has come under fire by interest groups concerned primarily about the non-commodity values (e.g., wildlife and fish, recreation) of National Forests. These groups charge that commodity interests' operations in the National Forests preclude other uses and reduce the amenity values of the forests.

There are several possible explanations for these challenges to the doctrine of multiple use and sustained yield. One is that both commodity uses and amenity values are compatible -- the problem is mismanagement by the Forest Service. Another might be that these values and uses are not all compatible; therefore, choices need to be made between competing uses, and the Forest Service does not have adequate direction from Congress for making those choices. A third view is that these conflicts are an outgrowth of changes in societal values as to whether **wildland** resources should be valued primarily for commodity uses or for their amenity values. In this case, the conflicts about uses of Forest Service land are, in a sense, part of a larger societal debate resulting from changes in held values about the environment.

Outdoor recreation is problematic in this regard -- it can be considered both an amenity and a commodity. Recreational opportunities are often considered to be amenities, yet in many cases, recreational opportunities can be bought and sold. Some conflicts about appropriate uses of Forest Service land include conflict over the types of recreation allowed. Environmentalists have opposed locating certain types of recreational establishments (such as ski resorts) on National Forest land. Other groups have opposed the establishment of wilderness areas, which exclude motorized recreation.

Recreation is one of the increasingly important "outputs" of National Forests. Recreational use of Arizona's National Forests is exceeded only by forests in California and Oregon, and recreation has been acknowledged as one of the primary products of managed forests in the Southwest (USDA Forest Service 1991a).

One important aspect of outdoor recreation is wildlife-related recreation. The Fish and Wildlife Service's 1985 national survey of fishing, hunting, and wildlife-associated recreation reported that 77% of the adult population took part in these activities (U.S. Fish and Wildlife Service 1988). Public interest in wildlife resources is high (Shaw et al. 1985), and this interest is one of the forces in many of the current controversies about National Forest management. Therefore, conflicts over recreation and types of recreation often become intermingled with conflicts over wildlife and maintenance of wildlife habitat.

Case study

To investigate Forest Service decisionmaking for an area where both outdoor recreation and wildlife are important amenity values or products of the forest, I chose to examine decisions being made about recreation management in Cave Creek.

Cave Creek Canyon on the eastern side of the Chiricahua Mountains is an internationally known site which attracts birdwatchers from all over the U.S. and the world. A 1979 survey indicated that, although many people came to Cave Creek to engage in wildlife-related recreation, 80% of the visitor groups surveyed came primarily for general outdoor recreation (e.g., hiking, camping, picnicking, driving for pleasure) (Shaw et al. 1979).

The camping facilities at Cave Creek Canyon are Civilian Conservation Corp vintage; no new campgrounds have been constructed since the 1930's (USDA Forest Service 1991b). The Coronado National Forest's 1986 Land and Resource Management Plan has prescriptions for Cave Creek for both the biological resources and the recreational facilities: the South Fork of Cave Creek was designated as a Zoological-Botanical Area; some of the campgrounds were slated for reconstruction; and the Plan suggested that an environmental education program be started in Cave Creek Canyon (USDA Forest Service 1986).

Rather than implement the Forest Plan prescriptions on a project-by-project basis, the Forest Service's Douglas Ranger District began (in the fall of 1990) to develop a Master Plan for Cave Creek. A Master Plan would set the tone of recreation management for the whole canyon.

The Douglas District Ranger allowed me to observe the interdisciplinary (ID) team meetings which were held as part of the planning process. The purpose of having an interdisciplinary team is to bring a range of expertise to bear on a natural resource problem. It was the job of the ID team to identify issues and concerns regarding the management of Cave Creek Canyon and to develop some alternatives. ID teams can include both Forest Service personnel and other parties concerned about or affected by the decision to be made. In this case, the team included both Forest Service employees and Portal-area residents. Residents represented various interests concerned about or affected by the management of Cave Creek Canyon.

As part of the ID team's work, the Forest's Landscape Architect developed six "visions" of recreation development in Cave Creek, spanning the range from increasing the number and size of campgrounds (estimated maximum Canyon occupancy up to 1,750 people at one time) to reducing campground number and size and emphasizing day-use (maximum occupancy of 225 people at one time). Public input regarding these "visions" and on Cave Creek management was solicited via a questionnaire. The questionnaire was distributed two ways: through an "open house" at which the 6 "visions" were displayed and Service employees were available for discussion, and through mailings to people and groups who had previously expressed interest and concern about the area's management.

Results and discussion

As expressed by the questionnaires and letters the Service received in March and April of 1991, most of the current users do not want to see change in Cave Creek Canyon. Of the 68 questionnaires and letters received, 56 (82%) expressed a strong interest in nature study and wildlife-related recreation and stated that the Canyon should be left as is -- additional recreation development should be minimal or non-existent. Fifteen (22%) of the respondents expressed interest in facilities which might represent increased recreational development: ramadas, equestrian trails, sewage disposal stations, group ramadas, guided tours, additional parking, landscaped areas, or biking trails. Of those 15 respondents who expressed interest in more recreational facilities, eight expressed a "no more development, leave it as it is" sentiment. (Four respondents (6%) expressed no opinion about recreation development.)

In contrast, the Forest Service thinks that change is inevitable, citing the fact that Arizona's population increased 40% from 1975 to 1985 (USDA Forest Service 1991a). The Service assumes that recreational demand in Cave Creek is and will continue to increase.

My observations last spring -- observing the ID team meetings, talking to the participants, attending the open house, and reviewing the questionnaires and written comments submitted to the Forest Service -- have allowed me to identify issues of concern to both the public and the Forest Service regarding the management of Cave Creek. Some of those include: the appropriateness of mining exploration in the area, the Forest Service's Sky Island National Recreation Area proposal, road and bridge improvements, the appropriateness of grazing in the Canyon, maintaining the unique biota of the area, maintaining the aesthetic qualities of Cave Creek, appropriate types of recreational use, conflicts between different recreational users, the appropriateness of attracting more users, how and from what viewpoint to define "too many" users, recreational impacts on the resources, distrust of the Forest Service, resistance to change, and recreational facility improvements or development.

In addition, I have identified groups and individuals (both inside and outside the agency) who attempt to influence the decisions made about Cave Creek management or who are clearly affected by those decisions. Those include: local residents, cabin lease holders, district-level Forest Service managers, forest-level Forest Service managers, letter writers, grazing permitees, members of coalitions, commercial and non-commercial tour operators, tour participants, researchers, and recreationists. (I am choosing at this time to exclude mining operators, since the Newmont mine exploration site is actually outside of the geographic area considered by the ID team.)

Future research

Reviewing the questionnaires received by the Forest Service generates questions. How representative are the respondents? Do their positions and attitudes adequately reflect the range of Cave Creek Canyon users? Are there some silent group or groups who have different issues and concerns? How can the Forest Service assess the concerns of people who do not use the Canyon because they want more facilities? How can the Forest Service assess the concerns of those who will stop using the Canyon if changes are made? Are these groups' concerns being expressed to the Forest Service or are they just "voting with their feet?"

As a result of this preliminary study, I have become interested in determining how various institutions and constituencies influence Forest Service policy regarding wildlife and recreation resources. I am interested in answering several questions: how do the expressed concerns of groups and individuals (both in and outside of the agency) influence the Forest Service's decisionmaking? Are non-agency groups and individuals representative of the public at large, or at least the users of the particular area under consideration? To what degree is Forest Service decisionmaking altered just because a particular area is in the public eye?

Because management policy regarding Cave Creek is actively undergoing change, Cave Creek is an ideal case study. To answer some of these questions, William W. Shaw, David A. King, and I will begin a survey of Cave Creek Canyon users this May. The survey will provide a profile of the Canyon's current users -- who they are, where they come from, what activities they pursue, what qualities of Cave Creek are important to them (e.g., wildlife, scenic beauty, scientific value, opportunity for primitive camping). Our survey will also incorporate questions about attitudes and knowledge and opinion of current management issues in Cave Creek.

In addition, we are developing a survey to assess the same things -- attitudes, knowledge and opinions about management -- for the groups who actively try to influence management or are affected by the management of the Canyon.

Acknowledgements

I thank Jeanne Wade, Gary Helbing and the other members of the ID team, Mitchel McClaran, David King, William Shaw, and Karl Flessa. This work was supported in part by McIntire-Stennis Project No. 139019-M-12-068.

Literature Cited

Shaw, W.W., T. Cooper, and M. Richards. 1979. *Recreational and scientific activity in Cave Creek Canyon, Chiricahua Mountains, Arizona 1978-79.* Final report prepared for the Coronado National Forest, USDA Forest Service, Tucson, AZ.

Shaw, W.W., W.R. Mangun, and J.R. Lyons. 1985. Residential enjoyment of wildlife resources by Americans. *Leisure Sciences* 7:361-375.

U.S. Fish and Wildlife Service. 1988. *1985 national survey of fishing, hunting, and wildlife-associated recreation.* U.S. Department of the Interior. Washington, D.C.

USDA Forest Service. 1986. *Coronado National Forest plan.* Printed with amendment pages, 1988. Southwestern Region.

USDA Forest Service. 1991a. *Arizona Recreation Initiative, an update ....* Southwestern Region.

USDA Forest Service. 1991b. *Cave Creek - Pinery corridor concept plan.* Draft, August 1991. Douglas Ranger District, Coronado National Forest.

A REVIEW OF GEOGRAPHIC INFORMATION SYSTEMS, AIRBORNE VIDEO REMOTE SENSING TECHNOLOGY RESEARCH, AND POTENTIAL APPLICATIONS IN CHIRICAHUA NATIONAL MONUMENT

Michael R. Kunzmann
Cooperative National Park Resources Studies Unit, University of Arizona, Tucson, Arizona 85721
Lee Graham and Dana Slaymaker
Advanced Resources Technology Laboratory, University of Arizona, Tucson, Arizona 85721

Introduction

The National Park Service (NPS) Cooperative National Park Resources Studies Unit (CPSU) and the Advanced Resources Technology (ART) group at the University of Arizona (UA) are constructing numerous Geographical Information System (GIS) databases for Chiricahua National Monument (CHIR) (Potter et al. 1992). Reliable Global Positioning Systems (GPS) data are critical in developing adequate GIS applications and testing the effectiveness of existing spatial correlation models that are used to evaluate, monitor, or document the existing conditions of natural and cultural resources.

Adequate GPS information is also required to evaluate and register historical maps and photos so that historically significant data or imagery can be incorporated into existing GIS applications and predictive models. Adequate evaluation and documentation of past and present resource conditions coupled with predictions of future resource conditions are required to meet current NPS research and management objectives. The efficient use of comprehensive resource evaluation and monitoring technology and systems such as GIS/GPS is considered to be of prime importance to the conservation, protection, and preservation mandates of NPS.

The GPS-Video system, was initially developed by the U.S. Forest Service (USFS) and the ART Laboratory (Myhre et. al. 1991). Current advancements in airborne video systems research by the laboratory have created two options for interfacing GPS technology to airborne video imagery (Graham et al. [1992]). Option 1 records the GPS data as a caption on each video frame. Option 2 utilizes a cost-effective Horita time code generator to encode computer-retrievable GPS positional information onto one of the videotape's audio channels. Subsequently, time-code-position information hierarchial indexing systems can be created and used to select, search, and capture the desired video frames. Post-digital processing permits direct transfer of these images into a variety of image-processing formats for subsequent image coordinate registration. After coordinate registration, the images can be incorporated into other GIS thematic data and imagery or exported to several target GIS and image-processing packages (GRASS, MIPS, EPPL7, IDRISI, and ERDAS) for additional processing. Once imagery data has been registered and transferred into the GIS, analytical comparisons between current imagery and historical data can be conducted on a routine cost-effective basis.

Conclusions and Further Research

Global Positioning Systems-linked airborne video technologies are currently being examined to provide low-cost imagery for a wide variety of research and resource management applications. Examples of current or potential GIS/GPS projects or applications that are being utilized or could be adapted to the Chiricahua Mountain area and CHIR are (1) vegetation mapping and management (Graham and Walsh [1992]); (2) fire history, behavior, and effects modeling (Ball and Gimblett in press, Ball and Guertin in press, Ball et al. in press, Kunzmann et al. 1991); (3) madrean habitat characterization and analysis (Bennett and Kunzmann 1992); (4) evaluation and monitoring of CHIR lang-term natural areas and ecological sites (Moir 1972); (5) construction of breeding bird atlases (Johnson and Kunzmann 1991);

(6) prediction of forage production and utilization (Wissler and Guertin 1991), (7) examination of the effects of Digital Elevational Model algorithms on viewshed analyses (Christopherson et al. in press), (8) development of archeological site prediction models (Kvamme 1989); (9) evaluation of historical map accuracies; and (10) a host of other management derived applications (Carroll et al. 1991). In addition, potential Chiricahua Mountains ecological data sharing linkages between the CPSU-UA and the U.S. Fish and Wildlife Service Arizona GAP Program and the U.S. Environmental Protection Agency Environmental Monitoring Assessment Program (EMAP) are being developed to lower the development costs associated with GIS and GPS and to facilitate information transfer between adjacent land-managing agencies in the greater Chiricahua Mountains area.

Literature Cited

Ball, G. L, and R. H. Gimblett. In press. Spatial dynamic emergent hierarchies simulation and assessment system. *Ecological Modeling* Special Issue: Ecological systems theory and modeling.

Ball, G. L, and D. P. Guertin. In press. Improvements in fire growth modeling. *Journal of Wildland Fire.*

Ball, G. L., D. P. Guertin, and M. R. Kunzmann. In press. Modeling fire behavior and effects using a geographic information system. In *Proceedings of the first biennial conference on research in Colorado Plateau National Parks, Northern Arizona University, Flagstaff AZ, July 22-24, 1991.*

Bennett, P. S., and M. R. Kunzmann. 1992. The applicability of generalized fire prescriptions to the burning of madrean evergreen forest and woodland. *Journal of the Arizona-Nevada Academy of Science* 24-25:79-84.

Carroll, C. S., S. A. Morain, L. R. Berger, and A. W. Berger. 1991. GIS derived biophysical land units (BLU) for change detection and resource management. Pages 206-221 *in* G. J. Buhyoff, editor. *Proceedings: resource technology 90: second international symposium on advanced technology in natural resources management, Georgetown University Conference Center, Washington, D.C., November 12-15, 1990.* Amer. Soc. for Photo. and Remote Sens., 5410 Grosvenor Lane, Bethesda, MD 20814.

Christopherson, G. L., D. P. Guertin, M. R. Kunzmann, K. L. Kvamme, and T. Potter. In press. The affect of DEM interpolation algorithms on viewshed analysis. In *Proceedings of the first biennial conference on research on Colorado Plateau national parks, Northern Arizona University, Flagstaff AZ, Ju 22-24, 1991.*

Graham, L., and J. Walsh. 1992. Applications and accuracy of GPS-linked airborne video for resource evaluation and mapping. (Submitted to the *Journal of Photogrammetry and Remote Sensing* for 1992 publication).

Graham, L, J. Walsh, S. Drake, C. Li, and D. Slaymaker. 1992. GPS-linked airborne video for resource evaluation & mapping. (Submitted to *International Journal of Remote Sensing* for 1992 publication).

Johnson, R. R., and M. R. Kunzmann. 1991. GIS and construction of breeding bird atlases for riparian/wetland ecosystems. Pages 498-506 *in* G. J. Buhyoff, editor. *Proceedings: resource technology 90: second international symposium on advanced technology in natural resources management, Georgetown University Conference Center, Washington, D.C., November 12-15, 1990.* Amer. Soc. for Photo. and Remote Sens., 5410 Grosvenor Lane, Bethesda, MD 20814.

Kunzmann, M. R., P. S. Bennett, and G. L. Ball. 1991. The use of ecological modeling in geographical information systems: the prediction of LD50 species mortality from fire intensity. ?ages 118-127 *in* G. J. Buhyoff, editor. *Proceedings: resource technology 90: second international symposium on advanced* *technology in natural resources management, Georgetown University Conference Center, Washington, D.C., November 12-15, 1990.* Amer. Soc. for Photo. and Remote Sens., 5410 Grosvenor Lane, Bethesda, MD 20814.

Kvamme, K. L 1989. Geographic information systems in regional archaeological research and data management. Pages 139-203 *in* M.B. Schitten, editor. *Archaeological Method and Theory,* Vol 1, University of Arizona Press, Tucson, AZ, USA.

Moir, W. H. 1972. Natural areas. *Science* 177:396-400.

Myhre, R. J., L Graham, and C. Sumpter. 1991. Airborne videography: a potential tool for resource managers. Pages 590-594 *in* G. J. Buhyoff. *Proceedings: resource technology 90: second international symposium on advanced technology in natural resources management, Georgetown University Conference Center, Washington, D.C., November 12-15, 1990.* Amer. Soc. for Photo. and Remote Sens., 5410 Grosvenor Lane, Bethesda, MD 20814.

Potter, T., M. R. Kunzmann, and D. P. Guertin. 1992. GIS program initiated at the U/AZ CPSU. *Park Science* 12(1):18-20.

Wissler, C., and D. P. Guertin. 1991. A spatial modeling approach to predicting forage production and utilization in a semidesert grassland. Pages 617-627 *in* G. J. Buhyoff, editor. *Proceedings: resource technology 90: second international symposium on advanced technology in natural resources management, Georgetown University Conference Center, Washington, D.C., November 12-15, 1990.* Amer. Soc. for Photo. and Remote Sens., 5410 Grosvenor Lane, Bethesda, MD 20814.

UNITED STATES
DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
ECOLOGICAL SERVICES
3616 W. Thomas, Suite 6
Phoenix, Arizona 85019

PARTNERS FOR WILDLIFE

Sam F. Spiller presented by
Kirke A. King

The U.S. Fish and Wildlife Service (FWS) will be initiating the Partners for Wildlife program in Arizona similar to on-going programs that are already started in Oklahoma and Texas. This new program is aimed at developing voluntary partnerships with willing private landowners to protect, restore, and enhance important fish and wildlife habitats, including those for endangered species.

The goal of the protection and restoration efforts is to maintain, improve, and reestablish species diversity for the State of Arizona. Priority is given to areas of importance for Federal endangered and threatened species, species under consideration for future Federal protection, and threatened native wildlife as designated by the Arizona Game and Fish Department as well as other declining species. Neotropical migrant songbird needs will be given priority as a diminished species group due to current National concerns. We want to improve protection and restoration of habitats in a manner that supports ecosystem maintenance.

Program emphasis is to be placed on restoration of natural vegetation systems in support of species biological diversity. In Arizona, the FWS wants to use Partners for Wildlife to protect riparian habitats, cienegas and other marsh-type wetlands, and key habitats such as special grasslands or other upland sites having special values.

The Partners for Wildlife plan will be developed with Arizona Game and Fish Department, Arizona State Parks, Native Americans, The Nature Conservancy and other entities, especially private landowners. The conceptual plan for Arizona will identify key areas of concern that may provide opportunities to formulate cooperative agreements with willing landowners interested in participating.

Current possibilities for protection and restoration may include fencing to protect riparian or marsh vegetation, pole plantings to reestablish riparian vegetation, and water control structures and earthen berms to reestablish aquatic and moist soil conditions for springs and cienega restoration. The FWS wants to emphasize the need to design agreements that are compatible with landowners interests, as again, this is a cooperative program based on willing landowner participants. Possible partnerships may result in the FWS funding improvements with the landowner carrying out the work and management. We also have capability to provide technical assistance for management plans that could then be carried out by willing landowners. State conservation agencies and conservation organizations may also become participants providing funding or labor.

If the FWS can be of further assistance regarding this program or if someone has some suggestions as to potential pilots projects, please advise Frank Baucom or Sam Spiller at our Phoenix Field Office, 3616 W. Thomas Road., Suite 6, Phoenix, Arizona 85019 (Telephone: 602/379-4720).

LICHENS AS BIOMONITORS OF AIR QUALITY IN THE CHIRICAHUA MOUNTAINS OF ARIZONA

Larry L. St. Clair and Clayton C. Newberry
Department of Botany, Brigham Young University, Provo, Utah 84602

Introduction

The first lichenological investigation in southeastern Arizona was conducted by Robert Darrow in 1950. He listed only 22 foliose, corticolous lichen species for the Chiricahua Mountains, a number substantially short of the total. Thirteen years later William Weber (1963) reported a total of 185 species in 50 genera for the Chiricahua Mountains. During the last two decades, the extensive collections and literature reviews of Dr. Tom Nash at Arizona State University have yielded a total of over 500 lichen species for the state of Arizona (Nash 1973, 1974, 1975, 1985). Adjusting for overlap between Darrow's and Weber's reports, at least 40% of the lichens of Arizona occur within the Chiricahua Mountains.

Geology, mountainous relief and monsoonal climatic patterns have created diverse habitats in Cochise County. The Chiricahua Mountains are composed of Oligocene tuff overlying Paleozoic and Mesozoic strata. Elevation ranges from 985 m to almost 3077 m. Plant communities vary with elevation, starting with Chihuahuan grassland in the lower slopes of the mountains, followed by encinal and inland chaparral. Montane to subalpine coniferous forests, composed of both Rocky Mountain and Sierra Madrean elements richly intermingled, occupy the higher elevations. With a maximum elevation slightly over 3000 m (at approximately 31° north latitude), a true timberline is lacking. Precipitation is biseasonal, with winter snowfall and summer monsoons. Late summer to early fall chubascos also occur, but less frequently.

The use of lichens as bioindicators of air quality is a well-documented procedure (Fields & St. Clair 1984; St. Clair 1989; Rope and Pearson 1990). Hale (1983) noted that lichens have been used in three ways to monitor the effects of air pollution on biological systems: 1) elemental analysis of lichen tissues, 2) mapping of all (or selected) lichen species found in areas adjacent to pollution sources, and 3) transplant studies. Currently, the most common approach involves floristic surveys along with elemental analyses of tissues from selected indicator species (St. Clair 1989; Wetmore 1989).

As lichens accumulate many different pollutants from atmospheric outwash, lichen tissues provide a record of the kinds and relative quantities of air pollutants in any particular airshed (Schutte 1977; Wetmore 1989; Rope and Pearson 1990). Pollution patterns for specific elements can be monitored over time by correlating thallus growth rates and pollutant concentrations in excised portions of the thallus (Lawrey & Hale 1981). Changes in lichen physiological processes indicate pollution-related damage long before other, more easily detectable changes in thallus color, morphology, or community structure become apparent (Fields & St. Clair 1984).

Lists of pollution-sensitive lichen species have commonly been published in conjunction with floristic and ecological surveys (Rushforth et al. 1982; Wetmore 1989). As certain lichen species from particular substrates are inherently more sensitive to airborne contaminants, air quality can be effectively monitored by occasionally reevaluating lichen community and/or physiological parameters. Pollution-related changes can then be documented by comparing follow-up data to original baseline data.

In the fall of 1990 the authors obtained funding from the U.S. Forest Service to make preliminary collections of lichens from seven class I wilderness areas throughout the state of Arizona. The purpose of this work was to gather data to be used for establishment of a preliminary air quality biomonitoring baseline in each wilderness area. In the Chiricahuas, as time did not allow a thorough survey of the entire wilderness area, we focused on three sites in the northern sector of the wilderness (Fig. 1).

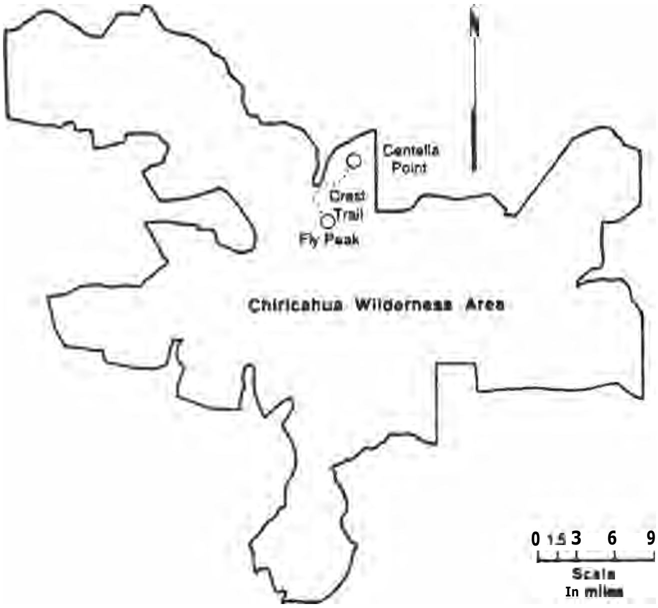


Figure 1. Map of the Chiricahua Wilderness Area, Cochise County, Arizona.

Based on current research into the sensitivity of lichens to air pollution, eight species from the wilderness area were designated as sensitive indicator species, including Dermatocarpon *miniatum*, Pseudevernia intensa, Ramalina pollinaria, Rhizoplaca chrysoleuca, Usnea hirta, Xanthoparmelia coloradoensis and Xanthoparmelia cumberlandia. Tissues of three of the pollution sensitive species were analyzed for concentrations of lead, sulfur and copper.

Probable pollution sources impacting the Chiricahua Wilderness Area are the copper smelters in Morenci, AZ, San Manuel, AZ, Playas NM, and Nacozari, Sonora. In addition, both the Tucson metropolitan area and the Apache coal-fired power generating facility near St. David may contribute to regional air pollution. In the past, air quality in the wilderness was probably impacted by the now-defunct copper smelter near Bisbee, AZ.

Conclusions and further research

In the three areas sampled, we collected 122 species in 48 genera. This number represents an unusually high species count for only three days' collecting in three small areas, and indicates a rich assemblage of lichen species. Among these collections were five new records for the state of Arizona: Bryoria simplicior, Hypocenomyce castaneocinerea, Pannaria tavaresii, *Pertusaria* albescens and Xanthoparmelia neotaractica.

The lichen flora of the Chiricahua Mountains is rich and apparently healthy. Corticolous species (52% or 64 species) dominate the flora at higher elevations. Most of the corticolous species, and also many of the saxicolous species, are foliose in growth form (43% or 50 species), a condition typical of many of the higher elevation lichen floras in New Mexico and Arizona. Fruticose lichens account for 8% of the total lichen flora-- a smaller percentage of the total number of lichen taxa despite the abundance of three very conspicuous species (Pseudevernia intensa, Usnea arizonica, U. cavernosa). Probably the monsoonal moisture patterns of southwestern North America are favorable to both fruticose and foliose growth forms. The microlichen flora is also diverse and well developed, but as yet somewhat poorly known.

Based upon Darrow's, Weber's and the authors' collections, the current species list for the Chiricahua Mountains includes over 200 species. We estimate that these 200+ species represent approximately 50-60% of the actual number of lichen species in the greater Chiricahua biogeographic area.

Sulfur concentrations in two indicator species Xanthoparmelia cumberlandia (0.217%) and Pseudevernia intensa (0.19%) are very close to chronic levels (Table 1).

Table 1. Elemental analysis data for selected species of lichens from Chiricahua Wilderness Area, Arizona. Means and ranges for each element are shown.

Species	Pb (ppm)	Cu (ppm)	S (%)
Pseudevernia intensa	48 (40-55)	60 (53-68)	0.19 (0.17-0.21)
Xanthoparmelia cumberlandia	70 (60-78)	34.8 (30-41)	0.217 (0.16-0.29)
Usnea subfloridana	39.8 (35-46)	25 (22-28)	0.16 (0.15-0.18)

This level of accumulation suggests the need for careful biomonitoring of sulfur dioxide in the wilderness. Evaluation of other parameters (e.g., membrane permeability and chlorophyll-phaeophytin ratios) for sensitive indicator species may be helpful in obtaining a more accurate understanding of the current condition of the lichen flora.

The Chiricahua Mountains support one of the most diverse and complicated lichen floras in western North America. The proximity of this magnificent resource to chronic air pollution sources necessitates that a comprehensive survey of the lichen flora be completed as soon as possible. In both the monument and the wilderness, also in the foothills and adjacent grasslands, regular reevaluation of the status of the lichen flora relative to air pollution impact is essential.

Literature Cited

Darrow, R. A. 1950. The arboreal lichen flora of southeastern Arizona. American Midland Naturalist 42: 484-502.

Fields, R. D. and L. L. St. Clair. 1984. A comparison of methods for evaluating SO_2 impact on selected lichen species: *Parmelia chlorochroa, Collema polycarpon and Lecanora mural is.* **The Bryologist 87: 297-301.**

Hale, M. E. 1983. The Biology of Lichens. Arnold Publishers, London.

Lawrey, J. D. and M. E. Hale. 1981. Retrospective study of lichen lead accumulation in the northeastern United States. The Bryologist 84: 449-456.

Nash, T. H. 1973. Additions to the lichen flora of Arizona I. The Bryologist 76: 545-548.

Nash, T. H. and W. A. Weber. 1974. Additions to the lichen flora of Arizona II. The Bryologist 77: 472-474.

Nash, T. H. and A. B. Johnsen. 1975. Catalog of the lichens of Arizona. The Bryologist 78: 7-24.

Nash, T. H. 1985. Additions to the lichen flora of Arizona III. The Bryologist 88: 19-22.

Rope, S. K. and L. C. Pearson. 1990. Lichens as air pollution biomonitors in a semiarid environment in Idaho. The Bryologist 93: 50-61.

Rushforth, S. R., L. L. St. Clair, J. D. Brotherson and G. T. Nebeker. 1982. Lichen community structure in Zion National Park. The Bryologist 85: 185-192.

Schutte, J. A. 1977. Chromium in two corticolous lichens from Ohio and West Virginia. The Bryologist 80: 279-283.

St. Clair, L. L. 1989. Report concerning the establishment of a lichen biomonitoring program for the Jarbidge Wilderness Area, Humboldt National Forest, Nevada, U.S. Forest Service Technical Report.

Weber, W. A. 1963. Lichens of the Chiricahua Mountains, Arizona. University of Colorado Studies Biological Series 10:1-27.

Wetmore, C. M. 1989. Lichens and air quality in Cuyahoga Valley National Recreation Area, Ohio. The Bryologist 92: 273-281.

SOME MODELING APPROACHES
TO THE ECOLOGY OF MOUNTAIN ISLANDS

ON THE MEASURE OF ORDER AND DISORDER IN THE DISTRIBUTION OF SPECIES ON ARCHIPELAGOS

Wirt Atmar, AICS Research, Inc.
PO Box 4691, University Park, NM 88003 USA

Bruce D. Patterson, Division of Mammals
Field Museum of Natural History
Roosevelt Road at Lake Shore Drive, Chicago, IL 60605 USA

Introduction

Extinction has been typically regarded as a highly stochastic process. It has been therefore surprising to repeatedly find patterns of extinction in natural communities which are pronouncedly deterministic (Brown 1986). Patterson and Atmar (1986, Patterson 1987) developed a statistical test to demonstrate the existence of non-random patterns of species distributions in ecological communities on archipelagos. The thesis underlying the test, which presumes "faunal relaxation", is simple: an archipelago of suitable habitats, inhabited by a common ancestral biota, is fragmented by climatic change. In these communities, some species will be more at risk of extinction than others. As area shrinks—for whatever reason—local populations will tend to go extinct in order of extinction risk. Quite often, the order will only be slightly perturbed by the statistical noise of local catastrophe. Immigration into depauperate areas will exhibit somewhat the same form of nesting, although on shorter time-scales and with less definitiveness. Certain species will be the first to invade, ordered by their species-typical vagilities. Other species follow only when a basic minimal trophic structure exists.

The measure of order and disorder in archipelagic communities

The metric to be described here measures the degree of order (and disorder) in species compositions on archipelagos, and to a degree, reverses the perspective taken in Patterson and Atmar (1986). The earlier metric, *N*, was devised merely to demonstrate that species distributions on an archipelago are not generally random. This demonstration was accomplished through the use of 1000-run Monte Carlo simulations, where n species were randomly distributed on m islands under two constraints, one mild and one tight. The programs to generate the random distributions were called RANDOMO and RANDOM1, respectively. Natural species distributions on "landbridge" archipelagos which are in the process of faunal relaxation were shown to be (very) significantly more ordered than either of the simulated random distributions.

The Patterson and Atmar (1986) metric was, however, incomplete and possessed several significant deficiencies as a practical measure. The value *N* was obtained by counting the number of absences of species from islands when the islands and species were arranged in nested order. This counting scheme has several shortcomings: (1) the count emphasized unexpected presences more than absences, (2) all absences were given equal weight, and (3) the *N* metric was matrix-size dependent (number of islands x number of species), thus a calculated *N* value could not be compared between archipelagos.

The metric described here corrects these problems. The metric is a measure of unexpected absences and presences and is similar to Cutler's (1991) measure of unexpectedness, but is different in its details of implementation. *Unexpectedness is* a concept closely related to the notions of information, entropy, and signal-to-noise ratios. Clausius first defined entropy as that fraction of unordered energy that is lost to an inaccessible pool of heat in every ordered energy transaction. The word *entropy* means means "in a turn", as in a gear. Boltzmann almost immediately redefined Clausius' entropy, S, as the degree of disorder within a population. Seventy years later, Shannon again redefined entropy as an informational measure of *surprise, I.* A signal-to-noise ratio (SNR) is the ratio of order to disorder in a system. The unexpected presence or absence of a species is clearly a similar idea to informational surprise. But the fundamental question is the most obvious: if unexpectedness is to be measured, how is *expectedness* to be defined?

If ordered extinctions exist, then a set of rules must also exist. As in all circumstances, a mixture of randomness and order constrains every physical process. It is however the general nature of even the most complex empirical observations that natural patterns result from the influences of only a very few first-order effects. Second- and third-order processes, which might otherwise contribute to the patterns, are often obscured by random noise and make no real contribution to the patterns observed.

The first order-effects which can be presumed to govern the extinction and immigration of archipelagic communities are simple and well-known: island size is a primary determinant of sustainable ecological diversity for three commonly argued reasons: (1) larger habitat sizes, (2) a more diverse suite of habitats, and (3) increased "passive" sampling. Populations are susceptible to extinction in a manner that is strongly determined by their relative population sizes. Large populations are resistant to extinction. Small populations, in contrast, are persistently subject to random extinction by environmental, demographic, or genetic vagary.

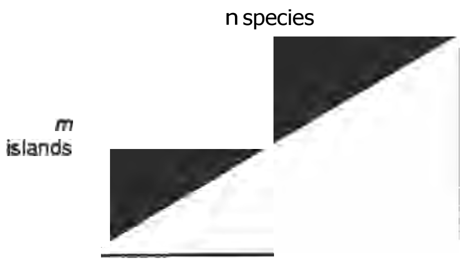
The argument for finding a highly ordered sequence of extinction in a progressively constricted community is therefore simple. The constituent species of an ecological community are not unlike electron shells surrounding a nucleus, bound to the islands of the archipelago with varying "strengths of attraction". As the community is constrained to increasingly smaller areas, species should be stripped away in a specific order. Top predators, specialists, and large-body forms are especially at risk. These species will characteristically have the smallest relative population sizes. As island size shrinks, their relative population sizes not only concommitantly decrease, but so do the sizes of their requisite habitats. An intrinsic ordering occurs as area is constricted. As one species disappears, another takes its place "on the bubble" as the next most susceptible to extinction.

Immigration into a defaunated area presumes a different process, but one that may be only slightly less ordered. Defaunated habitats are initially inhabitable by only a very few species. However, the probability of immigration into the defaunated habitat for the initial species is likely to be quite high. Only when the basal species have become established in sufficient numbers does the area become attractive to the next shell of member species, and then the next, etc., until ultimately the complete community has come to exist.

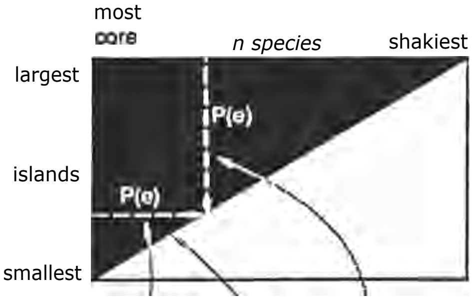
Neither of these two situations are in equilibrium for an isolated ecological system. The ordering that exists is transitory in time. Therein lies the profound value of archipelgos. Archiplegic populations which were derived the same source fauna and are distributed across random island sizes "stop" time in mid-sequence. The intermediate equilibrial states of the source fauna on variously-sized islands cleave the community structure into a sequence of progressively nested distributions. Because species persistence is so strongly tied to sustainable population size, and therefore island size, carefully chosen archipelagos (real or virtual) offer the chance of discerning relative extinction risks in a natural assemblage of species, information which would be very difficult to obtain by any other means.

The definition of *U*

Consider an m x n species-island presence-absence matrix of arbitrarily large size. Presences will be marked with a black square, absences with white. A *perfectly nested* matrix is defined to be one where every island contains a proper subset of the species of the islands above it, in ranked order. A *maximally nested* matrix, as shown, is a special case of a perfectly nested matrix in that no reordering of islands or species is possible and still maintain the same degree of system order.



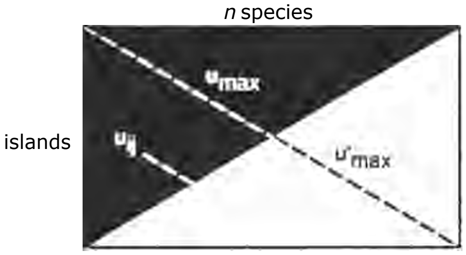
The presence or absence of a species on an island is not without meaning, and thus not without informational content. Species patterns on islands cannot be presumed to be arbitrary. A species may be regarded as a solution to a complex optimization problem, existing only where its ecological needs are satisfied by the local biotic and abiotic environment.



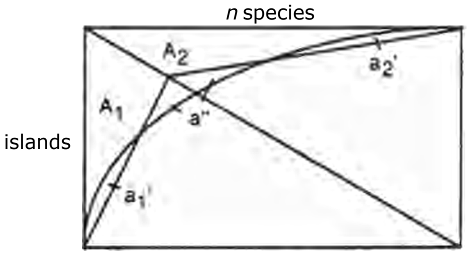
For a given island, the maximally nested matrix orders the species in terms of their increasing extinction probabilities, left to right. The "shakiesr will always be the rightmost species in a maximally nested matrix.

The probability, P(e), of extinction for a given species is increased as its population size decreases, in ordered sequence from top to bottom.

The line that separates the occupied area of the matrix from the unoccupied may be called the "extinction boundary'. Species on this line are at or near minimum population levels and are at great risk of extinction.



Unexpectedness is measured in the direction of the skew diagonal and is scaled to the length of the maximum line that runs through species



To describe the extinction line for a perfectly ordered system of arbitrary fill, the smoothest line (maximum order) is drawn in the manner described in the text and shown above.

In every community of species distributed across an archipelago of homogenous islands, there will be one species which will be the most core (most resistant to extinction). Similarly, for any given island size, there will be one species which is nearest to its minimum sustainable population size, and thus at greatest risk of extinction. An observed ordered presence-absence matrix can be viewed as an empirical representation of the extinction/immigration probability order for that specific community of species, island-by-island.

The diagonal line that separates the occupied areas of the matrix from the unoccupied can be called with equal accuracy either the "extinction boundary" or the "50-50 line". The extinction of a species resident on the line would carry little or no surprise, and thus no information. In contrast, the extinction of the species from the island in the upper-left corner of the matrix (the most core species) would be most unexpected. The same degree of surprise would be similarly characteristic of the unexpected appearance in the next epoch of the species in the lower-right-hand corner of the matrix.

Unexpectedness therefore runs diagonally, parallel to the skew diagonal of the matrix. Unexpectedness is measured by the distance of an unexpected presence or absence of a species from the 50-50 line, and would seem to increase faster than its simple linear distance. Therefore, let us define local unexpectedness as

$$u_{ij} = (d_{ij} / D_{ij})^2$$

where D_{ij} is the length of the entire diagonal which runs through the j^{th} species on the i^{th} island and d_{ij} is the specific length along that diagonal from the 50-50 line to the unexpected absence or presence. Total unexpectedness, U, may then be defined as

$$U = 1/(mn) \sum_i \sum_j u_j$$

The double normalization of the metric, U, results in a measure which is insensitive to the matrix's size or shape. A *perfectly ordered* matrix will have a $U = 0$. A matrix of maximum unexpectedness (a checkerboard pattern) will have a $U_{max} = 0.04145$. For purposes of presentation, the U score is normally scaled to 100% by taking the ratio, U/U_{max}.

The matrices drawn to this point have had a 50% fill (that is, 50% of the elements reflect species presences), but a nested matrix of perfect order exists for any arbitrary fill percentage. The determination of the 50-50 extinction line against which unexpectedness will be measured is straightforward and geometric. If the percentage fill of a matrix is *0,* then a point *OD* is chosen along the skew diagonal. Lines are extended to the opposite corners. The areas $A_1 + A_2$ equal the desired fill. Moreover, $A_1 = A_2$. A line of smoothest transition is then drawn from corner to corner such that the areas $a_1' + a_2' = a''$. The line of smoothest transition will also be the line of maximum order, where *order* is defined by degree of impact that the rearrangement of any two islands or species would have on the divergence of U from the absolute minimum.

A maximally nested matrix takes on the quality of a very wet liquid, forming a meniscus in the upper-left corner of the matrix. The constituent species of the community possess some degree of internal cohesiveness, but will also spread through the system's islands under a spreading pressure. Furthermore, the perfectly nested matrix assumes the attributes of a very cold liquid, such that perfect order occurs only at zero temperature. As the temperature (extrinsically imposed randomness) is raised, a turbulence (noise) is imposed on the structure and the line between perfect presences and perfect absences becomes increasingly blurred. A gray band replaces the distinct black/white demarcation of the perfectly ordered matrix.

The U score is the measure of the width of the gray band, and is therefore also a measure of the ratio of the disorder to order in the community-island matrix. External disruptions will take two forms: (1) the random variation of local catastrophe, and (2) events disconnected from the primary extinction/immigration event. Consider a "relaxing" fauna undergoing extinction by continued areal constriction. If (1) the internal cohesiveness of the community is high, (2) the level of local catastrophe is small, and (3) the archipelago is isolated from immigrating species, the order of the system will be quite high and the U score low. But if "turbulent" mixing is pronounced, local extinctions and unexpected presences will broaden the width of the gray band uniformly along the entire extinction boundary. In contrast, if post-isolation immigration is common, certain species will appear on a subset of the islands, biased to those islands which are closest to their respective sources. The two forms of divergence from perfect order may be segregated by these patterns in the following manner: an idiosyncratic species—a species disconnected from the primary extinction/immigration event—may be detected by defining an idiosyncratic index, 1, as

$$1(j) = 1/m \; {}_{i} \; u_{ij}$$

where u_{ij} is defined as before. If $I(j)$ is at or near the value of U, then the jth species is likely to have been a member of the original community of species on the archipelago. But if $1(j)$ diverges much from U, then the species must be declared to be somehow idiosyncratic to the general event governing species presences on the archipelago. The practical value of the metrics I and U allow (1) the assessment of extinction risk for individual species and (2) the opportunity to unravel a portion of the historical biogeography of the archipelago.

Acknowlegements

This work resulted from a study group held at the Southwestern Research Station, Portal in March, 1991 and owes much to the collaborative efforts of the group. The group was composed of Alan Cutler (Chicago, then Arizona), David Wright (Emory, then Georgia), Greg Mikkelson (Chicago), and the authors. Support for the work was provided by AICS Research, the Field Museum, and NSF grant BSR-9106981 to BDP.

Literature Cited

Brown, J.H. 1986. Two decades of interaction between the MacArthur-Wilson model and the complexities of mammalian distributions. *Biological Journal of the Linnean Society*, 28: 231-251.

Cutler, A. 1991. Nested faunas and extinction in fragmented habitats. *Conservation Biology*, 5: 496-505.

Patterson, B.D. 1987. The principle of nested subsets and its implications for biological conservation. *Conservation Biology*, 1: 323-334.

Patterson, B.D. and W. Atmar. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. Pages 65-82 in L.R. Heany and B.D. Patterson, editors. *Island biogeography of mammals.* Academic Press, London.

ON THE ROLE OF MALES

Wirt Atmar
AICS Research, Inc., PO Box 4691
University Park, NM 88003 USA

Introduction

The existence and value of males has for some time been considered an enigma. Gender differentiation is not equivalent to sex. A broad array of hypotheses for the evolution and persistence of sexuality appears in Michod & Levin (1988). Yet for all postulated arguments, males are unneccessary. While purpose cannot always be easily ascribed to a specific trait or behavior, the converse can be argued with confidence. The widespread, common existence of a specific trait or behavior insures that the attribute possesses purpose.

Protracted demonstrations of competitive vigor are common in males, especially so in polygynous species. "It is incredible that all this should be purposeless" (Darwin 1874, p. 615). The hypotheses to be argued here are threefold: (1) males are an auxiliary, relatively sacrificial sex of enhanced fragility, whose demonstrations of competitive vigor operate to expose, exaggerate, and expurgate significant gene error from the germline, (2) the aggressively competitive behavior of polygynous males is but one component of a hierarchy of genetic information assurance mechanisms that must be inevitably evolved, and (3) gene defect expurgation from the germline greatly accelerates the evolutionary optimization, and thus the competitiveness, of the species.

The relationship of replicative error to complexity

Progressively increasing complexity characterizes evolution because it is the simplest and most probable (thermodynamically "cheapest") mechanism for evolving increasingly large reservoirs of complex behavior. Simple informational structures cannot encode complex behaviors. Nor can complexity be built in one step. Metamerism and exaption are the great tricks of evolution, where one set of encoded structures or behaviors is duplicated and reoptimized for alternate purposes, to be used in a hierarchical internal alphabet. In higher-order evolutionary sequences, it is the changing *relative* expression of a large collection of behavioral "objects" that represents the majority of evolution, not changes in the basal objects themselves.

There is however a critical upper limit to the complexity level that may be evolved given a fixed mutational error rate. The governing inequality is

$$> p$$

where n is the number of actively translated loci, μ' the basal thermodynamic error rate per locus, and p the ploidy (redundancy) number. Should *ng* much exceed p, then error will accrue in the population faster than any possible level of selection can cull it from the germline. If $\gg p$, no individual progeny will exist without significant mutational deviation from its parent. Reproduction must be very nearly replication if the ancient lineage of phylogenetically accrued knowledge is to be maintained. If that linkage is significantly broken at every replication, the evolutionary search decays into a condition worse than enumeration. One of three choices is presented to evolutionary design: (1) limit n, and thus limit complexity, (2) evolve mechanisms which reduce the effective mutational error rate, μ', or (3) greatly increase redundancy (polyploidy). Complexity above a prescribed limit cannot be evolved in the absence of the evolution of error suppression and recovery mechanisms.

Sexual selection

In 1859, and again in 1871, Darwin defined two forms of stringent populational culling, *natural* and *sexual*. Natural selection is the sum of all competitive culling phenomena which are *extrinsically im-*

posed on the evolving phyletic line. But the second form of selection, sexual, is evolved *within* the lineage itself. The processes are not the same, nor are the effects. Natural selection moves a population of variants across an adaptive topography to a local optimum by means of the selective culling of the least fit. In contrast, sexual selection works to maintain the quality of the information phylogenetically accumulated in the species-typical genome. The populational genetic effect of intense and prolonged male-male intrasexual contest is the exclusion of measurably defective variants from the breeding population, prior to mating. Primary congenital defects often exhibit pronouncedly debilitating effects on their bearers. The "genetic" death of a defective allele is as potent an error suppression mechanism as physiological death, if it is vigorously enforced with a concommitant ethology.

There exist only three simple mechanisms of information assurance: repair, redundancy, and stringent testings of vigor. Redundancy (polyploidy) increases the probability of proper genotypic expression by mitigating the effects of an uncorrected point mutation. The expression of an alternate, functional allele is often sufficient to maintain the viability, if not full competitiveness, of the individual phenotype. But redundancy is an informational trap to the species. To maintain the informational integrity of the genome through an infinite number of replications, the level of redundancy must also grow to infinity, but at a faster rate than the number of replications. Redundancy levels above diploidy cannot be argued to be an effective escape mechanism from thermodynamically inevitable informational decay. High-p polyploidy is very rare in plants and virtually unknown in animals.

In contrast, the evolution of mechanisms of repair and stringent testing must be considered to be inevitable. The observed mutation rate, μ, is not the basal thermodynamic error rate affecting germline DNA, but is rather the residual error rate uncorrected by existing the internal error repair mechanisms of the cell. Repair mechanisms, by their nature, cannot be precise and are intrinsically incomplete. The evolution of any repair algorithm is a constrained process, where error comes to be recognized in the packetization of the code, not in the actual message itself. Nor can a finite set of error repair algorithms detect and repair all forms of error. Some error will pass uncorrected.

The only mechanism available to the species to directly assess the quality of the message contained within the inherited genome is the stringent vigor testing of (at least) a subset of its phenotypes. Complex physiologies are often brought to a halt through a single "well placed" point mutation. A defect is informationally trivial and isolated from the remainder of the genome, and is subject to a highly directed selection in a manner that no complex, integrated functional behavior can be. Absolute fitness is an immeasurable quality, but the relative fitness of individual phenotypes is easily assessed in prolonged contest.

The single metric—sustained, demonstrable vigor—integrates a great deal of information over a diverse range of qualities. It is a measure of the individual phenotypes's sensory acuity, the capacity to avoid predation, immune system compentancy, general intelligence, and foraging behavior. The simple demonstration of vigor in a sexually mature adult is a highly integrative measure of overall phenotypic quality, providing reasonable assurance that the individual phenotype is free of primary congenital defect. The efficiency of the defect expurgation process from the germline does not need to be extreme to be effective. The effect is multiplicatively regenerative, generation after generation, honing species-specific variances to levels at or near environmental noise.

The acceleration of optimization

There exists a third attribute characteristic of the evolution of error reduction mechanisms (repair and vigor demonstrations) that has been very little discussed. The exclusion of macromutational error from the germline dramatically accelerates the optimization of the phyletic lineage. The practical advantages of reducing phenotypic variance as optimality is approached have been repetitively demonstrated in simulated evolutionary algorithms for engineering optimization purposes (e.g., Fogel et al. 1990, Fogel et al. 1991). Although the process may initially seem counterintutitive, the stabilization of genetic information accelerates evolutionary optimization by reducing the effects of unconstrained mutation. Collapsing the variance of a normally-distributed mutagenesis function increases the density of trials by a factor of (at $/\sigma_t)$, where σ_t is the characteristic variance of the state vector at time *t* and n the rank of the trial vector. Because n (number of loci) is often very large, small changes in a produce large volumetric changes in the state space which is to be probablistically explored (Atmar 1990). A similar argument has been commonly made in entomological genetics for the advantageous evolution of haplodiploidy: (1) the ready exposure of defects in the male, (2) the instrinic resistance to the deleterious effects of inbreeding in haplodiploids, and (3) the rapidity of local race formation (e.g., Hoy 1985).

Enhancing the expurgation rate

If defects are to be efficiently exposed and expurgated from germline DNA through male-male contest, then the evolution of physiological mechansims to enhance the exposure of defects from the germline must be expected to permeate phenotypic design. The evolution of adult haploid males especially exaggerates the opportunity to expose significant gene error in the complete genome. The filtering nature of haplodiploidy is clear. Alleles in a haplodiploid mating system are exposed to selection on the basis of the gender caste through which they pass. A lethal or subvital allele in the ovum of a diploid female is not informationally equivalent to a spermatozoic lethal derived from a hemizygotic male. Indeed, the spermatozoic lethal cannot exist by definition.

Gender is a sexual platform on which extensive behavioral and phyiological differentiation has been imposed. Haplodiploid males are physiologically extremely fragile by virtue of their genetic construction, but much evidence exists that most diploid males are similarly more physiologically fragile than their conspecific females. Polygynous diploid males generally succumb more readily to disease, trauma, exhaustion and starvation; suffer higher embryonic mortality rates; die in greater numbers from accident and intrasexual combat; bear higher parasitic worm loads; live shorter lives or are driven from the population after breeding. Polygynous males rarely care for their young or participate in the economy of the species and become especially dispensible in times of ecological stress.

Explicit genetical mechanisms, such as haplodiploidy, which very efficiently expose error in males, do not appear to be wholly necessary. The evolution of combative behavior in the diploid male appears sufficient. Metabolic exhaustion is a common theme in polygynous male sexual behavior. If a defect can be exposed, **it** will be made most apparent under metabolic stress. The intrasexual contest has generally evolved to be as rigorous a demonstration of vigor as possible. Feeding is usually suspended prior to and during the period of male-male combat, tending to increase overall metabolic stress further (Kodric-Brown & Brown 1984, 1987; Atmar 1991, and references therein).

Darwin was fully aware that human males are more variable than females, and more physiologically fragile. "...a vast number of measurements was made of various parts of the body in different races, and the men were found in almost every case to present a greater range of variation than the women...The cause of this general variability in the male sex than in the female is unknown, except so far as secondary sexual characters are extraordinarily variable, and are usually confined to males." (1874 pp. 223-224). "Prof. Faye remarks that '...the fact is, that for every 100 still-born females, we have in several countries from 134.6 to 144.9 still-born males. During the first four or five years of life, also, more male children die than females; for example in England, during the first year, 126 boys die for every 100 girls—a proportion which in France is still more unfavourable...Dr. Stark also remarks that 'These examples may suffice to shew that, at almost every stage of life, the males in Scotland have a greater liability to death and a higher death-rate than the females. The fact, however, of this peculiarity being most strongly developed at that infantile period of life when the dress, food, and general treatment of both sexes are alike, seems to prove that the higher male death-rate is an impressed, natural, and constitutional pecularity due to sex alone'." (1874 p. 243).

Vigor testing obtains maximal value only when the code set under consideration is irredundant. All known eukaryotes engage some form of nuclear ploidy cycling, normally alternating diploid and haploid stages. Diploidy is a chromosomal redundancy state which apparently rests robustly between counterbalancing forces. Diploidy is the lowest ploidy state which will allow sexually-mediated chromosomal recombination; diploidy is simultaneously the highest ploidy state that can be reduced to haploidy in one meiotic step. When informationally reduced, uncovered, hemizygotic alleles directly expose latent gene defects to selection, if translated in the haploid state.

Male gametes are produced in far greater numbers than their corresponding ova. Sperm/egg ratios in the higher primates average ibout 100 million:1 per copulation. In both Metazoa and Metaphyta, sperm and pollen are smaller, more motile, more energy-restricted and placed more immediately at risk than the egg. Only one male gamete is paired with one ovum. All other sperm are functionally dispensible. The human vagina/cervix is an environment that is generally considered hostile to sperm. Sperm appear to be required to run migration paths of evolutionarily enhanced stringency as a profound demonstration of basal cellular metabolism. Rigorous competition significantly reduces the probability that the single fertilizing spermatozoon will be maabolically impaired, have an abnormal chromosomal complement, or be otherwise incompetent.

Evolution is a physical information-transforming process, subject to only a very few rules. Parthenogenetic clonality, the informational schema which builds all multicellular phenotypes, leads to rapid and inescapable senescence in less than a few hundred replications. If the species, especially an informationally complex species, is to outlive its cells, mechanisms of information protection must be evolved. The evolution of rigorous competitions in a relatively sacrificial subpopulation is a solution that partially satisfies the critical necessity of providing a mechanism for the protection and maintenance of the information accumulated within the species' genome. In that, the behavior of the adult polygynous male recapitulates much of the function and informational value of his sperm.

Literature cited

Atmar, W. 1990. Natural processes which accelerate the evolutionary search. Pages 1030-1035 in R. Chen, editor. *Conference Record, 24th Asilomar Conference on Signals, Systems & Computers.* IEEE Computer Society/Maple Press, San Jose, California.

Atmar, W. 1991. On the role of males. *Animal Behaviour,* 41: 195-205.

Darwin, C.R. 1874. *The Descent of Man and Selection in Relation to Sex.* 2nd Ed. Reprinted 1896, D. Appleton & Co., New York.

Fogel, D.B., L.J. Fogel, and V.W. Porto. 1990. Evolving neural networks. *Biological Cybernetics,* 63: 487-493.

Fogel, D.B., L.J. Fogel, and W. Atmar. 1991. Meta-evolutionary programming. Pages 540-545 in R. Chen, editor. *Conference Record, 25th Asilomar Conference on Signals, Systems & Computers.* IEEE Computer Society/Maple Press, San Jose, California.

Hoy, M.A. 1985. Recent advances in genetics and genetic improvement of the Phytoseiidae. *Annual Review of Entomology,* 30: 345-370.

Kodric-Brown, A. and J.H. Brown. 1984. Truth in advertising: the kinds of traits favored by sexual selection. *American Naturalist,* 124: 309-323.

Kodric-Brown, A. and J.H. Brown. 1987. Anisogamy, sexual selection, and the evolution and maintenance of sex. *Evolutionary Ecology,* 2: 209-224.

Michod, R.E. & Levin, B.R. 1988. *The Evolution of Sex.* Sinauer Associates Inc., Sunderland, Massachusetts.