# Bats of the Madrean Archipelago (Sky Islands): Current Knowledge, Future Directions

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**Abstract.**—Twenty-three bat species occur in Arizona's Sky Islands. Each one has specific, seasonally changing requirements for roosts, forage and water. Current knowledge about these species is insufficient for informed ecosystem management. We pose research questions and suggest techniques and resources for answering some of these questions. Managers, in cooperation with researchers, should establish long-term plans and priorities for studying and monitoring bats.

# INTRODUCTION

Bats are vital members of most terrestrial ecosystems, yet frequently are ignored in vertebrate surveys and ecological evaluations. Worldwide, bats occupy every major feeding niche except herbivory (Stebbings 1980). Insectivorous bats are major predators of nightflying insects. Other bat species, especially in the tropics, consume nectar and/or fruit. Many are important pollinators and seed dispersers (Cox *et al.* 1991, Gardner 1977).

This paper addresses concerns and responsibilities of those charged with ecosystem management. A key to management is recognition of species diversity. One cannot manage generally for "bats" any more than for "birds." Just as spotted owls, elegant trogons, and Mexican chickadees are each studied and protected within the context of their particular habitats and individual requirements, so must the biology of each bat species be understood to determine its needs.

Although bats comprise nearly a quarter of all mammalian species, our knowledge of most of them is fragmentary. Perhaps because they fly, are nocturnal, and are mostly unseen, bats are among the least studied mammal groups. For most species we know neither total range nor accurate population numbers. We know even less about their ecology and life history. Indications are that most bat species worldwide are probably declining in numbers due to several causes, including losses of habitat, roosts and food, direct or indirect killing by humans, and harmful effects of chemicals (Stebbings 1980).

As Cockrum (pers. comm.) has noted, many past estimates of bat populations, plus speculation about their life histories, came from incidental natural history observations made as part of general biological surveys, most often on summer field trips, and frequently by observers with little expertise in identifying species and estimating numbers. Information on reproductive status, sex ratios, and roost types often was not recorded. For many species we know only general food requirements, such as "insectivorous," but not specific prey or feeding strategies, or "nectarivorous," but not exact plant requirements through different seasons and habitats.

# BACKGROUND

Sustaining ecosystem diversity necessitates meeting the individual needs of each species. Three basic requirements of all bat species are: 1) appropriate roosts for their various seasonal and reproductive activities, 2) suitable foraging areas, and 3) adequate water. For each species, these needs are satisfied differently. Variation also occurs within a species, between populations or across geographic regions. The specifics of these requirements for each bat species are relevant to management considerations. Particulars of the three requirements follow.

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#### Roosts

With few defenses against predators, most bats survive by escaping detection in roosting sites and by restricting their activity to the night. By roosting in sheltered places, bats are protected from predators, large temperature fluctuations, and adverse weather conditions. Roosts also enhance activities such as rearing young, digestion of food, social interactions, and hibernation (Kunz 1982).

In describing types of shelters (as introduced by Verschuren), Gaisler (1979) lists as major distinctions:

- 1) "external" or "internal," based on "degree of isolation from the macro-habitat," and
- 2) composed of vegetation, rock or manmade structures, based on environmental conditions of the roost. We would add
- colonial or solitary, based on tendency of individuals to cluster;
- day, night, or transient, based on length of time or portion of 24-hour period spent in the shelter;
- 5) maternity, bachelor, or hibernaculum, based on gender or physiological condition; and
- 6) summer or winter, based on season.

Few bats use the same day roost throughout the year; the annual cycle usually includes seasonal movements among different roosts. Many species roost in caves or mines, some use rock or tree crevices, others seek cover in tree foliage, and some take shelter in manmade structures such as buildings and bridges. Some bats roost singly, while others aggregate in colonies. Each species has specific humidity and temperature requirements for its roosting sites, which may change seasonally — not just any dark, quiet place will do. Most caves and mines, for instance, do not qualify as either good hibernacula or nursery roosts. Therefore, when bats are disturbed and driven from a roost, they may be unable to find another suitable retreat. Or, if they are able to move within the same cave, for example, the alternate site may not be satisfactory for long-term survival of that population.

Many bats appear to have high individual fidelity to roost sites, returning to the same site year after year. For some species that have been studied, populations appear to be limited by availability of suitable roost sites, and disturbance or destruction of these sites by human activity is a principal cause of population decline. (Kunz 1982.)

# Forage

Bats spend a substantial portion of their lives away from their roosts feeding. For insectivorous bats, this activity typically entails flying over a defined area in a "search pattern" hunting for prey. Prey items usually consist of night-flying insects, but for some species include ground-dwelling arthropods such as crickets and scorpions. Two non-insectivorous Arizona batspecies feed primarily on agave nectar and on cactus nectar and fruits.

Geographic areas in which bats forage are defined by abundance of food. For example, individuals of *Macrotus californicus* will fly along desert washes (P. Brown pers. comm.) where there is a higher concentration of a primary prey item, grasshoppers. Myotis yumanensis forages over streams where it feeds on adult forms of aquatic insects (Brigham et al. 1992). Different species use various capture techniques and may feed at different levels of the canopy or in different subsections of the habitat (Neuweiler 1984). Some food partitioning occurs, as different species divide an area specially and tend to consume different sizes or taxa of insects (Herd and Fenton 1983). Extent and location of foraging territories varies according to bat species, seasonal abundance and variety of food, and changing energetic and dietary requirements. A bat's foraging territory may be close to the day roost, or may be many miles distant.

Foraging requirements as well as major roosting sites must be made secure before a bat species is adequately protected. Too often, roost sites are the only aspect of a bat's natural history considered when attempting to protect them. Roost and food requirements should be considered together. Although foraging ecology of a bat species is usually much more difficult to study than roosting ecology, it is equally important to the survival of the animals.

#### Water

Most bat species need a supply of free water every night during active periods. Water sources are typically ponds, streams, or cattle tanks. Bats drink by flying just above the water, skimming the surface with their jaw or tongue. Different species require different configurations of water source. Some species need a long unencumbered approach to drink, whereas more maneuverable ones can drink from steep-sided tanks, tinajas and even wells. Most bats probably utilize the nearest suitable source of water. In dry seasons, this may be some distance from the day roost and/or feeding area. A few species, such as those feeding on nectar and fruit, acquire most of their water from their food. As with roosts and forage, lack of water sources could be a limiting factor on some bat populations.

# **BATS OF THE SKY ISLANDS**

Sky Island ecosystems constitute a unique biological crossroads. Of the 44 bat species found in the United States, 28 have been recorded in Arizona, and 23 of these are known to occur in the Sky Islands during at least part of the year. Although none of these species is limited to the Madrean Archipelago, the high diversity of bat species is likely due to the diversity of habitats, including desert grassland, Chihuahuan desertscrub, encinal and Mexican oak-pine woodland, and montane conifer forests (Lowe and Brown 1973), in conjunction with deciduous riparian zones, year-round water, and steep rock-walled canyons.<sup>3</sup> Different habitats support different assemblages of species. The topography of the Madrean Archipelago, in which habitats usually separated by large latitudinal distances are brought into close proximity, may also influence species diversity.

# **Records of Bats in the Sky Islands**

Table 1 lists the 23 bat species recorded from the Sky Islands (nomenclature per Jones *et al.* 1992). While this discussion is limited to that part of the Madrean Archipelago which lies in Arizona, management implications should be the same either side of the border.

Hoffmeister (1986) tabulates relative distribution of mammals of Arizona by vegetative community, based on percentage of total number of localities from which records exist for each species. Thirteen vegetative communities are listed, of which three, desert grassland, oak-pine woodland, and montane conifer forest, predominate on Arizona Sky Islands. For twelve bat species (marked with an asterisk in Table 1), the highest percentage of localities occurs in one or more of the three communities, indicating significant association with Sky Island habitats.

Our understanding of most Sky Island bat species is incomplete. To summarize current knowledge, we look at evidence of bat use through the seasons. (Sources are Barbour and Davis 1969, Cockrum and Ordway 1959, Hoffmeister 1986, Cockrum pers. comm., SLS and DCD pers. obs.) Undoubtedly, as more information becomes available this picture will change.

Maternity roosts (individual or colonial) of Choeronycteris mexicana, Myotis velifer, M. thysanodes, M. volans, Lasiurus blossevillii, Plecotus townsendii and Antrozous pallidus have been observed in Arizona Sky Islands. Pregnant or lactating females of Myotis auriculus, M. californicus, Tadarida brasiliensis, and Nyctinomops *macrotis* have been recorded, suggesting that parturition occurs in the Sky Islands, but maternity roosts have not been found. Female Leptonycteris *curasoae*, collected in August and containing tiny embryos, likely give birth in Mexico (Cockrum and Ordway 1959). Maternity roosts of Myotis yumanensis, М. auriculus, M. volans, *M*. californicus, M. ciliolabrum, Pipistrellus hesperus, Lasiurus xanthinus, Lasiurus cinereus, and Idionycteris phyllotis have rarely or never been recorded and are not well understood. (Some of these species have been studied elsewhere, but nursery roosts are not well documented for the southwestern environment.)

Other summer records (adult males, non-reproductive females, or gender unreported) exist for Leptonycteris curasoae, Myotis velifer, M. auriculus, M. thysanodes, M. volans, M. californicus, M. ciliolabrum, Lasionycteris noctivagans, Pipistrellus hesperus, Eptesicus fuscus, Lasiurus blossevillii, Lasiurus cinereus, Idionycteris phyllotis, Plecotus townsendii, Antrozous pallidus, Tadarida brasiliensis, and Nyctinomops macrotis. Little is known about location and requirements of bachelor roosts for most of these species.

Migrating groups of *Leptonycteris curasoae* and *Tadarida brasiliensis* use transient roosts in the Sky Islands. Capture records of *Lasiurus cinereus* are significantly higher in spring, suggesting this species may stop over during migration. *Choeronycteris mexicana, Leptonycteris curasoae*, and most *Tadarida brasiliensis* are thought to winter in Mexico. It is not known to what localities particular populations of these species go, nor what transient habitats are important to their journey. (However, see Cockrum 1969.)

<sup>&</sup>lt;sup>3</sup>Also occurring on some Sky Islands, but more incidental, are Upper Sonoran desertscrub, chaparral and sub-alpine spruce-fir forest.

	ATERNITY ROOSTS <sup>2</sup>	PREG./ LACT. FEMALES <sup>3</sup>	OTHER SUMMER CAPTURES <sup>4</sup>	TRANSIENT ROOSTS <sup>5</sup>	WINTER RECORDS <sup>6</sup>	SCANT . RECORDS <sup>7</sup>	PERIPHERAL
Macrotus californicus					✓		✓
* Choeronycteris mexicana	✓				NA		
* Leptonycteris curasoae	NA	August	✓	✓	NA		
Myotis yumanensis						✓	
Myotis velifer	✓						
* Myotis auriculus		✓	✓				
* Myotis thysanodes	✓		✓				
* Myotis volans	✓		✓				
* Myotis californicus		✓	✓				
* Myotis ciliolabrum			✓				
* Lasionycteris noctivagana	NA		✓		✓		
Pipistrellus hesperus			✓				
* Eptesicus fuscus			✓		✓		
Lasiurus blossevillii	✓		✓				
* Lasiurus cinereus			✓				
Lasiurus xanthinus						✓	
* Idionycteris phyllotis			✓				
* Plecotus townsendii	✓		✓		✓		
Antrozous pallidus	✓		✓				
Tadarida brasiliensis		~	✓	✓	✓		
Nyctinomops femorosacc	us					✓	
Nyctinomops macrotis		✓	✓				
Eumops perotis						~	

Table 1.—Summary of known occurrences of the 23 bat species of the Sky Islands

# NOTES:

1) Species marked with an asterisk have the highest association with Sky Island vegetative communities (from Hoffmeister, 1986).

2) Actual maternity roosts have been located and identified in the Sky Islands for the checked species.

3) Reproductive females of the checked species have been captured in the Sky Islands, but no roosts located.

4) Males, non-reproductive females or unknowns of these species have been summer captured in Sky Islands.

5) Colonial roosts used for short periods of time seasonally are known in the Sky islands for these species.

6) Winter records of captures and/or roosts of these species exist for the Sky Islands.

7) There are a few records for these species from the Sky Islands, but they are not found regularly.

8) This species is found near to Sky Island habitats, but it is not known from the Sky Islands proper.

9) NA means that these categories are not applicable to this species in the Sky Islands.

A wintering aggregation of *Plecotus town*sendii has been found in one Chiricahua hibernaculum. Individual *P. townsendii* in winter torpor have also been located in several area mines and caves. Very likely other bat hibernacula occur in the Madrean Archipelago, but none have yet been found. Capture records document individuals of *Lasionycteris noctivagans, Eptesicus fuscus*, and *Tadarida brasiliensis* overwintering in the Sky Islands, but their winter roosts and requirements are largely unknown. From the often scant evidence he could accumulate for winter records, Hoffmeister (1970, p.12) observed "a tendency for most species of bats in Arizona either to move to the southeast corner of the state or to move out of the state altogether during the months of November through March." Even for such widespread and "common" species as *Myotis velifer, Myotis volans, Lasionycteris noctivagans* and *Antrozous pallidus,* where they go and what they do in winter remains a mystery.

Historic records of the following species are reported from Sky Island localities, but insufficient data are available to determine their status: *Myotis yumanensis, Lasiurus xanthinus, Nyctinomops femorosaccus* and *Eumops perotis*. A winter roost of *Macrotus californicus* is located at a low elevation on the periphery of a Sky Island, but this species does not appear to use Island habitats significantly.

# Questions to Answer for Informed Stewardship

Adequate information about a species is needed before protective measures can be taken. Because we do not have sufficient biological information on any of these species to ensure their survival, what questions should we be trying to answer for each bat species.

<u>Roosting Ecology</u>: Questions remain about lo-1) cations of roosts for many species. Most bat species are found in a variety of habitats. Do their roost requirements differ between various habitats or are they the same? Bats using caves and mines have traditionally been the most studied. However, many species use shelters such as rock or tree crevices or tree hollows where human detection has been difficult. Habitat components vital to bats may currently be unknown to us (Saugey 1991). Roost requirements are often poorly understood; for example, mines that seem to us to be perfectly suitable have no bats. To confound the fact that we probably have not yet found some critical roosts in the Sky Islands, we have no accurate method of predicting if a site would be a suitable roost. Until we do, all potential roosts must be examined (Altenbach pers. comm. See Kunz 1982 and Sheffield et al. 1992.)

Maternity roosts are particularly crucial. If maternity roosts are not secure, the population will not survive. Bats are especially vulnerable because of their low reproductive rate of one or two young per year in most species. Even a slight reduction in birth rate could have a significant impact on the population. Bats are also extremely vulnerable during hibernation, when arousal may cause depletion of energy reserves and lead to starvation (Mohr 1972).

2) Foraging Ecology: It is essential to understand foraging ecology as well as roosting ecology, because a different combination of environmental factors is required for each. Foraging ecology encompasses food habits, territory description and extent, necessary proximity of forage to roosts and water, and shift in dietary needs and/or foraging territory throughout the season. (See Fenton 1982 and Fleming 1982.) Not enough is known about foraging requirements of any Sky Island bat species.

- 3) <u>Seasonal Movements</u>: Migratory bats are similar to migratory birds in that an impact to a population at one of its seasonal homes may affect the community at the other. Understanding better the migratory patterns and seasonal movements of bats utilizing the Sky Islands will require, for some species, an international effort including Mexico and Canada.
- 4) <u>Reproductive Biology</u>: Although information exists about pregnancy, lactation and weaning for some species, mating systems and locations of mating are virtually unknown. This category of reproductive biology needs more attention. (See Bradbury 1977.) Variation in length of gestation, timing of parturition, and rate of development due to differing environmental or geographic conditions must also be considered (Orr 1970, Pearson *et al.* 1952).
- 5) <u>Population Status</u>: Are numbers increasing, stable, or declining? What keeps a given population from growing larger? Is it limited by shortage of suitable roosting sites, by lack of accessible food or water sources, or by confounding factors such as disease, predation or human activity (Pearson *et al.* 1952).
- 6) Importance to Ecosystem: The importance of bats in the ecosystem is poorly known for most species. An understanding of their relationships with other organisms is necessary for effective stewardship. As answers to the above questions clarify interrelationships within the web of living and non-living elements of the ecosystem, we can begin to investigate the role played by each species. (See Cox *et al.* 1991.)

# RESEARCH

Maintaining a healthy ecosystem requires gathering baseline data and then establishing regular monitoring protocols. We recommend that managers, in collaboration with researchers, examine long-term goals and concerns, and set priorities for monitoring systems. Many individual research projects are conducted for only one or a few seasons. The result is that our knowledge is fragmentary, especially if there are multiannual fluctuations in local population sizes. Managers of public lands have the opportunity to support both basic and applied research (species, population, community, or ecosystem questions) and to ensure that long-term monitoring occurs.

Clearly, we lack basic biological information on most bat species to manage for them. Acquiring such knowledge takes time and careful research design. In this section, we review a variety of methods used in field studies, offer examples where these techniques have been used to answer biological questions, and suggest research to pursue in the Sky Islands.

# **Field Methods**

The techniques discussed below answer different questions and each has its own limitations and biases. It is important to know these limitations and to use the techniques most appropriate for the objectives of the study. In addition, it must be realized that to handle bats or disturb them in their roosts inevitably introduces stress, and potentially shortens their lives (Stebbings 1966). Therefore, effort should always be made to maximize information gained from any study.

This overview is intended as an introduction to research methods, not as instruction for use of equipment nor training in application of techniques. Most basic methods are described in *Ecological and Behavioral Methods for the Study of Bats* (Kunz 1988), which must be supplemented with more recent literature for current information on each technique. Before undertaking a research project, it is necessary to determine which technique (or combination of techniques) is suitable to the question being asked, and to investigate available equipment.

Thomas and LaVal (1988) noted that bat researchers doing population studies often failed to specify and test assumptions, biases, and limitations inherent in the methods used. They urge that future quantitative population studies be conducted with increased rigor and reported with extreme caution, because inaccurate estimates, once published, tend to be repeated as "truth" (Thomas and LaVal 1988). These cautions are equally applicable to any research project. Poorly planned or executed field studies can result in major mistakes. Past examples of which we are aware include roost surveys conducted in the wrong season, leading to inaccurate population estimates, and a nursery roost gated in the middle of the maternity season, which caused a major disturbance to the bats the gate was intended to protect. Proper execution of each technique and correct interpretation of the results require, in most cases, considerable experience.

#### **Capture Devices**

*Harp traps* and *mist nets* are two devices used to capture bats in a particular location by intercepting them in flight (Kunz and Kurta 1988). Bats show differing abilities to detect and avoid nets and traps. The set of the net or trap, location selected, height of the net or trap above the ground, and environmental conditions of the particular night (moon, wind, temperature) will influence the catch. Failure to capture a particular species at a given time and place does not assure that the species was not present. The catch is not, therefore, a random sample of the population of bats in an area. Nevertheless, sufficiently large sample sizes over a long enough time can give a reasonable indication of relative abundance. The advantage to capture is the ability to identify species, sex, and reproductive status, and to make quantitative morphological measurements. Capturing a bat is also a necessary first step for many other techniques.

#### **Tracking Methods**

Three marking techniques, *radiotelemetry*, *light tagging* and *banding* are useful for tracking individual bats. (See Barclay and Bell 1988, Wilkinson and Bradbury 1988.) The principal difference between the three methods is the length of time one obtains information from a given marking. Light tagging only lasts for several hours in a single night. Radiotelemetry can last in excess of 20 days and banding can last for the lifetime of the bat.

Light tagging is used to locate roosts by tracking bats to them, and to conduct detailed studies of foraging strategies. Because the location of the light can be visually pinpointed, the bat's movements can be described in great detail. This technique has a limited range of only about 1 to 2 miles and it also requires a minimum of about 10 observers to be effective.

Although less precise than light tagging, particularly for observing foraging behavior and choice of food items, radiotelemetry provides longer-term information on nightly foraging strategies such as consistency (or inconsistency) of foraging patterns and distance traveled from the roost. Telemetry is also useful for locating roosts, especially those in places not traditionally investigated, such as tree cavities. Banding enables long term tracking of individuals to determine migration timing and patterns, longevity, behavior and alternate roost usage. Several different band types are available; the right type for the species being studied must be chosen. Banding of bats is problematic because of the difficulty of attaching the band in a manner that does not cause wing damage. It is important that field workers applying tracking devices to bats be skilled in the technique and informed on its risks and benefits.

#### **Roost Surveys and Censuses**

Under appropriate conditions, internal cave and mine surveys can be an effective method of locating and censusing bat roosts. (See Thomas and LaVal 1988.) However, abandoned mines may be quite dangerous to humans; caves can require a considerable amount of skill and time to survey; and bats being censused may be unduly disturbed by the human activity. The technique should only be undertaken by experienced bat biologists who are also skilled in caving techniques and mine safety. Mist netting (or trapping) and night-vision equipment can be used in place of internal surveys, or to supplement them.

#### **Fecal Analysis**

Guano analysis can aid in identification of food items. (See Whitaker 1988, Thomas 1988.) By periodically collecting samples throughout the season, changes in diet can be detected. Bat guano samples can also be analyzed for residues of agricultural pesticides and other chemicals (Reidinger 1972, Clark *et al. 1982*).

#### **Echolocation Monitoring**

Ultrasonic detection is a useful tool for assessing comparative habitat use and relative bat abundance (Thomas and LaVal 1988). (See also Barclay and Bell 1988, Fenton 1988.) The technique is used as an indicator of bat presence, followed by another technique, such as mist netting, for positive species identification. For surveys of free-ranging bats, this technique may have fewer biases than other sampling methods. It is appropriate for surveys, not censuses, because the number of bat passes is not an accurate indicator of the number of individuals. With a broadband microphone that picks up all frequencies, echolocation monitoring can be used in conjunction with mist netting as evidence of bats present but not captured. Caution must be exercised when attempting to identify bats to species level using ultrasonic detectors; several species in a given area may have ultrasonic signatures that overlap, and intraspecific variability also occurs (Thomas *et al.* 1987). †

#### Night-vision Equipment with Near-infrared Video

Night-vision devices (Barclay and Bell 1988), although quite expensive and easily damaged, have proved to be one of the primary tools of bat biologists for emergence counts and behavioral studies. For permanent record and removing observer bias, the night-vision device can be optically coupled to a video system and recorded on magnetic tape.

#### **Other Techniques**

Other research methods are available as well. Some are summarized in Kunz (1988). Newer techniques that show promise include DNA analysis and geographic information systems (GIS). DNA analysis from widely separated populations may reveal inter- or intraspecific kinships that would be difficult to determine by any other known technique. GIS, utilizing databases, can be used as a management tool for mapping out ranges and distributions of various species and correlating multiple factors for ecological relationships.

# **Examples of Information Gained**

These and other techniques are used by bat biologists to answer questions important when managing for species and ecosystems. The following reports of research from many localities illustrate information that can be obtained. Techniques used in these examples could be applied to studies in the Madrean Archipelago.

#### **Roost Location**

In a study of 200 mine features in New Mexico, 42 percent were found to be used by bats (Altenbach and Milford 1991). These included winter hibernacula for six species, nursery colonies of *Plecotus townsendii* and *Myotis thysanodes*, and a migratory stopover roost for *Myotis yumanensis*. Many of the mines had vertical entrances that required specialized equipment and trained personnel. This equipment and training permitted the field workers to discover these roost sites, which would have been undetected by external surveys.

- 2) An area of the Coronado National Forest containing numerous mines was surveyed for potential roosts. Using a combination of techniques including multi-season internal surveys, mist-netting at entrances, bat detectors and night-vision equipment, a significant usage of one of these mines by lesser long-nosed bats (*Leptonycteris curasoae*, protected as a federally endangered species) was discovered (unpubl. data). A superficial survey, or one in the wrong season, could easily have missed them. The land manager now has information to make decisions regarding future development of the site.
- 3) "Waves" of silver-haired bats (*Lasionycteris noctivagans*) travel along the southern shore of Lake Manitoba during spring migration (Barclay et al. 1988). Historical records suggested that this is generally a crevice-dwelling species, yet little was known of their roost sites because they had rarely been located. During May and June 1984-1986, two to four people conducted almost daily visual searches of trees along a 2-km stretch of ridge. They discovered 177 *L. noctivagans* (90% of which were females) located in 36 different roosts in 32 trees. Roosts typically were crevices in tree trunks: most commonly a narrow space behind folds in heavily furrowed bark, but also splits in tree trunks and narrow spaces between two touching trunks. (Barclay et al. 1988.)

It was not known whether females of this species rear their young in isolation or in aggregations. In Shasta County, CA in 1992, Rainey *et al.* (in press) captured reproductive female *Lasionycteris noctivagans* in mist nets over water. They attached radio transmitters to two of them and were able to track them to two day roosts located in tree cavities. Significantly, each roost contained more than 20 individuals. This supported the 1986 discovery in Ontario and Saskatchewan of two maternity colonies of the species also in tree cavities (Parsons *et al.* 1986), suggesting that during maternity season this bat roosts colonially rather than solitarily as previously thought.

# Seasonal Movements, Migration and Roost Fidelity

1) From a five-year banding study of Townsend's big-eared bats (*Plecotus townsendii*), Pearson *et al.* (1952) were able to determine that females in nursery colonies exhibited strong roost fidelity, returning to the same site each year. The longest migration distance recorded for these bats was 20 miles. One large cave housed both hibernating and maternity colonies of bats, but in different tunnels winter and summer. Furthermore, banded bats from other summer colonies appeared at this cave to hibernate. Finally, banding records were used to estimate an average age of five years for the populations they studied. (The authors reported precipitous declines, attributed to their disturbance of the bats, in some of these populations; an important cautionary note for anyone contemplating such a study. See also Pierson and Fellers 1993.)

2) Between 1952 and 1967, more than 168,000 Brazilian free-tailed bats (*Tadarida brasiliensis*) were banded at sites in Arizona and Mexico (Cockrum 1969). From the 2% recovered later plus data from other studies conducted in Oklahoma, Texas, New Mexico and California, Cockrum (1969, p. 324) concluded that "four or more behaviorally (and possibly genetically) separate populations of *Tadarida brasiliensis mexicana* occur in the western United States during the summer months." A recent electrophoretic study by McCracken *et al.* (1994) did not support the suggestion of genetically distinct populations.

# **Food Habits and Foraging Areas**

1) In 1986, Dalton *et al.* completed an analysis of guano collected for three years from a Plecotus townsendii virginianus roost (Dalton et al. 1986). About 97% of the bats' diet consisted of moths. This information set the stage for concern over gypsy moth management measures, since insecticide (Dimilin) used to control gypsy moths would also drastically reduce other lepidopteran species. Subsequently, Dalton et al. (1989) carried out a two year study on the foraging ecology of *P. t. virginianus*. Light tagging and radio tracking enabled researchers to identify foraging areas. Land manager foresight led to appropriate research, and the colony's critical foraging territory was worked into management

plans, which refrained from Dimilin use in those areas.

2) A foraging study was conducted in 1993 on a colony of *Leptonycteris curasoae* located near an active mining operation. Through light tagging, critical foraging areas for the bats were identified and plans for expansion of the mine were altered to accommodate these requirements (Dalton and Dalton 1994b).

#### Habitat Use

In forested mountains of Washington and Oregon, automated ultrasonic detector systems indicated that nearly all common bat species required forest stands for day roosts, apparently traveling to adjacent riparian habitats to feed. Roosting activity was many times higher in oldgrowth than in young or mature stands, presumably because large, old trees and snags offer the highest diversity and abundance of hollows for roosts (Thomas and West 1988). In a separate study, guano traps suspended in basal hollows of redwoods in California revealed extensive bat use of these old-growth trees for roosts during all seasons (Rainey *et al.* 1992).

# **In-roost Behavior and Population Trends**

- In 1991, the Air Force became concerned that their training flights in the vicinity of a *Leptonycteris curasoae* roost might be stressing the colony. Dalton and Dalton studied the bats' behavior while Air Force jets flew over the roost. The bats were recorded on video tape using infrared illumination and a night-vision device. In order to observe natural in-roost behavior with minimal disturbance to the bats, remote-controlled equipment was used. Statistical analysis of the video tapes showed no serious adverse effects on the bats. (Dalton and Dalton 1993)
- 2) In 1993 a federal agency adopted a census protocol for a large colony of *Leptonycteris curasoae* using night-vision and video recording equipment. This method allows the agency to monitor population trends at the roost and be aware of any problems before they become critical (Dalton and Dalton 1994a).

#### Pesticide Poisoning

In a recent European study, timber, feces and tissue samples were analyzed for pentachlorophe-

nol (PCP) residues, and a striking correlation was found between all three. The researchers concluded that the PCP burden of bats may be estimated from analysis of their droppings (Cordes 1994. See also Clark *et al.* 1982).

#### Suggested Research for the Sky Islands

The following are a few suggestions of specific problems that need solving in the Sky Islands. These questions are not necessarily more important than others, but do constitute a starting point.

#### **General Questions**

- Many historical records for bats in the Sky Islands were gathered from only a few well-known localities, such as Sabino Canyon in the Santa Catalinas and Cave Creek Canyon in the Chiricahuas. Attention needs to be directed toward less studied areas, such as forested uplands, and some of the less accessible mountain ranges.
- 2) Foraging ecology studies are urgently needed. Much information can be obtained on foraging ecology with available techniques. Bats can be tracked from known roosts, or captured while foraging (or drinking) and tracked to learn both roosting sites and foraging behavior.
- As mentioned, winter habits of most bat species in Arizona are unclear. (See Hoffmeister 1970.) The location of overwintering sites for the majority of bats remains a mystery.

#### **Ecosystem Questions**

- How does the topography of the Madrean Archipelago affect bats? Because several habitats occur in close proximity, all are potentially accessible to flying mammals. How do various bat species use these multiple habitats? Do any species undergo altitudinal migrations between seasons? Some evidence for this occurs among *Plecotus townsendii* in the Chiricahuas (DCD pers. obs.), and it has been suggested as a possibility for other species (Cockrum pers. comm., Hoffmeister 1970).
- 2) How does forest fire impact bat habitat? Is there a higher occurrence of potential tree roosts in burned areas or in old growth forest? Does fire suppression affect available roosts positively or negatively?

3) Do bats use the grasslands surrounding the montane islands? (Localities recorded by Hoffmeister 1986 indicate they do). Presumably these areas would be used for forage more than roosting sites. What are the effects of differing land use regimes on bat species? While revisiting historic bat roosts, Reidinger (1972) documented a trend toward decrease of available man-made and natural roosts with the increase in human population. He also observed harmful effects from insecticides. "In comparison with other Arizona mammals with residue values reported in the literature, bats suffer by far the greatest insecticide exposure" (Reidinger 1972, p. 137). Development, grazing and pesticides may all impact bat species which inhabit Sky Island habitats during at least part of the year.

# **Species Questions**

All species require more study. We have selected three, suggesting some questions that could be productively pursued.

1) Leptonycteris\_curasoae\_

Populations of *Leptonycteris curasoae*, a nectar-feeding bat, migrate annually into Arizona from Mexico. With individuals numbering into the tens of thousands in a single cave or mine roost, *L. curasoae* is a highly colonial species. Several important questions about this species remain unresolved. Since the predominant range of *L. curasoae* is in Mexico, studies on both sides of the border are needed.

> (Demographics) In late April and early May, а. gravid females arrive at three known maternity roosts in southern Arizona located west of the Sky Islands (Cockrum 1991). During the months of pregnancy and lactation, these females feed almost exclusively on columnar cacti such as saguaro and organ pipe. By late July, transient roosts at higher elevation sites in the Patagonia, Huachuca and Chiricahua mountains are occupied by a mixture of adult females and juveniles and some adult males. These seasonal movements appear to reflect a shift in available food resources from cacti to agaves (Cockrum 1991). It has not been determined whether populations occupying transient sites in the Sky Islands are the same ones found in Arizona maternity

roosts or are different populations flying northward from Mexico. Most individuals of *Leptonycteris curasoae* leave Arizona by late September or early October and migrate to overwintering sites south of southern Sonora (Cockrum 1991). The specific migration routes and winter roosts are unknown. In addition, the population status of the species is uncertain; are numbers increasing, decreasing, or stable?

- b. (Nectar corridor) Fleming *et al.* (1993) discovered that northern populations of the species feed almost exclusively on CAM plants, Cactaceae and Agavaceae, during summer and during their spring and fall migrations. This suggests that a nectar corridor of CAM plants exists along both of their postulated migration routes. Flowering periods of at least four species of columnar cacti coincide with the bats' northward progression in spring (Fleming et al. 1993). However, field studies are needed to confirm whether Agave flowering peaks in Mexico are coincident with passage of migrating bats in the fall, and whether the bats depend on these plants. If a nectar corridor indeed supports the seasonal migrations of *L. curasoae*, then loss of plant populations along either migration route could severely impact the bats (Fleming *et al.* 1993).
- c. (Bat/agave mutualism) Howell and Roth (1981) postulated an obligate mutualism between *Leptonycteris curasoae* and Agave palmeri, but their evidence has been disputed (Cockrum and Petryszyn 1991). Howell and Roth's (1981) conclusion was predicated on A. palmeri fruit set and seed set. However, a number of pollination biologists, examining resourcelimitation versus pollinator-limitation hypotheses, have suggested that fruit and seed set are not valid indicators of reproductive success in hermaphroditic out-crossing plants such as *Agave pal*meri (Stephenson 1984, Sutherland 1986, Sutherland 1987, Sutherland and Delph 1984, Udovic 1981). Pollination experiments are needed to test the bat/paniculate agave interdependency hypothesis.

It seems generally agreed that *Leptonycteris cura*soae is an important pollinator for *Agave palmeri*, and that *A. palmeri* is a major food source for populations of *L. curasoae* at higher elevations in southeastern Arizona during mid- to late-summer. However, further research must be done to clarify the extent of their interdependence. This information is important to the conservation of both bats and agaves.

- d. (Impact of hummingbird feeders) In many Sky Island localities in recent years, both Leptonycteris curasoae and Choeronycteris mexicana have been observed drinking sugar water from hummingbird feeders at night. Sightings have been made from April into October (Lee and Clark 1993). This phenomenon raises some concerns about the effect of this comparatively new food source on bats. If bats, particularly juveniles, depend too heavily on nutritionally-deficient sugar water, they may not have sufficient energy for migration. Some individuals may delay their migration and subsequently suffer from extreme weather. Feeders which provide a ready source of "food" could in reality be a population sink, if the animals become part of a positive feedback loop under conditions actually negative to their survival (Richter *et al.* 1993).
- e. (Reproductive biology) Very little is known of the reproductive biology of *Leptonycteris curasoae*. There is some evidence that parturition is asynchronous, with births reported at various times scattered through the year. The location, timing and system of mating for *L. curasoae* are also unknown (Fleming pers. comm.).
- f. (Chiricahua roosts) While most adult males of the species probably remain in Mexico during summer, by May some males are found in high-elevation roosts in the northern Chiricahua Mountains (Cockrum 1991, Cockrum and Petryszyn 1991, Fleming pers. comm.). The function and importance of these roosts need to be determined. Why, when the majority of males appears to remain in Mexico, does this population come to the Chiricahuas? Are Leptonycteris curasoae present in the Chiricahuas throughout the summer, and if so, is it the same population for the entire season. What food sources are

used by the bats before the flowering of Agave palmeri in late June? Not only does an influx of post-lactating females and juveniles occur at the Chiricahua sites in late summer, but records of reproductive males and newly gravid females captured at these roosts during August (Cockrum and Ordway 1959) also hint that these "transient" refuges may serve an additional role. It is possible the males found in southeastern Arizona may mate with some of the females from northern populations when they move to higher elevation roosts in August and September, before migrating southward. If so, caves and mines in Arizona Sky Islands could be important mating sites for the species (Fleming pers. comm.).

#### 2) Plecotus townsendii

- a. ("Alternate" roosts) In Arizona, Plecotus townsendii is a year-round inhabitant of caves and mines. In summer, females form colonies of up to a few hundred individuals to rear their young. Maternity colonies have been observed relocated in alternate roost sites in the middle of the maternity season. These "alternate" sites may be within the same cave/mine or nearby in a different one (Tipton 1984, Dalton and Dalton pers. obs.). What triggers these movements? Do the requirements of the colony change as the reproductive condition of the bats changes, or do the roost conditions change sufficiently to necessitate these movements? Without an answer to this question, a colony of *P. townsendii* could be lost from destruction of "alternate" roosts despite adequate protection of the "primary" roost.
- b. (Winter behavior) In winter, these bats hibernate in higher-elevation roosts which are colder than their summer roosts (DCD pers. obs.). Because milder climates are within nightly flying distance of potential hibernacula, *P. townsendii* in the Sky Islands may arouse periodically throughout the winter to forage at lower elevations. This sort of winter activity has been observed in California (Pearson *et al.* 1952, Pierson *et al.* 1991). A study could be conducted to determine if there are active *P. townsendii* foraging at lower elevations. If this be-

havior is confirmed, these animals could be used to locate new hibernacula higher in the mountains.

(Winter roost requirements) In the eastern c. United States, a different subspecies is known to hibernate in clusters in excess of 1000 individuals (C. Stihler pers. comm., DCD pers. obs.). Only one hibernaculum with a significant number of *Plecotus* townsendii is currently known in southern Arizona. Other southern Arizona winter sites have only a few to about twenty non-clustering individuals. In New Mexico, a similar pattern is observed, with bats usually hanging singly or in groups up to about ten, with the largest single cluster numbering about 100 (Altenbach pers. comm.). Is this scattering of individuals in winter typical of *P. town*sendii in Arizona, or conversely, are major hibernacula in the Sky Islands still undiscovered? If they are not colonial in winter, identifying roost requirements, and subsequently, determining management actions, become much more difficult.

#### 3) Lasionycteris noctivagans

In contrast to *Plecotus* and *Leptonycteris*, *Lasionycteris noctivagans* is a generally solitary species whose preferred day roosts are probably crevices in trees (Barclay et al. 1988). Cockrum and Petryszyn (n.d.) have summarized current knowledge about this species. It is seasonally abundant in the Chiricahua Mountains. There are no known records in adjacent northwest Mexico. Males have been recorded in Arizona in every month, but females only from October through June. No gravid females or juveniles have ever been recorded in Arizona. It is thought that females of the species migrate to coniferous forests in the northern U.S. and Canada to give birth and raise their young (Cockrum and Petryszyn n.d.). As best as can be reconstructed from current data, the northern range limit shifts north in summer and south in winter (Kunz 1982). .

Nearly a quarter of the *Lasionycteris noctivagans* reported for Arizona by Hoffmeister (1986) were netted during winter in the Chiricahua mountains. This fact, plus the absence of any records of the species south of the border, raises the possibility that the Chiricahuas may be a significant overwintering site (Cockrum pers. comm.). In New Mexico, an individual was caught in a mist net (i.e. was active and flying) at 28°F (Barbour and Davis 1969). Research into winter habits of this species is suggested.

#### CONCLUSION

Primary responsibility for protecting the health of Arizona Sky Islands falls to the agencies which administer these largely public tracts of land. Managers must concern themselves with all flora and fauna under their stewardship, leaving them little time to gain an in-depth knowledge of any one species. What are their best sources of information? Books and journals are of course the primary storehouse of knowledge about bats and bat research. A central database, such as that maintained by AGFD Heritage Program, is useful for some regionally specific facts, but is not always up to date. The most useful resources for current information are experienced bat biologists. Knowledge is always in flux. New discoveries disprove long accepted theories. Updated information mandates refinement of research and management strategies. Active bat specialists are most likely to keep up with such changes. Land managers can use the specialized knowledge of these individuals for effective management. Development of monitoring protocols and management plans should be undertaken in collaboration with researchers working in affected areas. Close, on-going cooperation between managers and researchers can lead to better decisions.

The issues involved in managing for bats are not simple. Understanding their relationships with other flora and fauna is central to understanding the natural diversity of the ecosystems in which they live. As example, bats directly affect the plants and insects that they utilize as food. Indirectly, those bats eating insects will have an effect on the plants upon which their insect prey feed. Therefore, it is necessary for zoologists, botanists and entomologists to work together to gain a more complete understanding of these interactions. To ignore ecological relationships is to oversimplify a naturally complex system. In the words of Janovy (1985), "As a role model for society, the biologist above every other kind of scientist should demonstrate the futility of searching for simplistic and purposeful answers to complex natural problems." This point is key to maintaining natural systems.

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# LITERATURE CITED

- ALTENBACH, J. S. and H. MILFORD. 1991. Evaluation and management of bats in abandoned mines in the southwest.BatRes.News32(4):63.
- BARCLAY, R. M. R. †ANDG. P. BELL. 1988. Marking and observational techniques. Pages 59-76 *in* T. H. Kunz, ed. Ecological and Behavioral Methods for the Study of Bats. Smithsonian Inst. Press, Wash. D.C.
- BARBOUR, R. W. AND W. H. DAVIS. 1969. Bats of America. University Press of Kentucky. 286pp.
- BRADBURY, J. W. 1977. Social organization and communication. Pages 1-72 *in* W. A. Wimsatt, ed. +Biology of Bats (III). Academic Press, New York.
- BRIGHAM, R. M., H. D. J. N. ALDRIDGE, R. L. MACKEY. 1992. Variation in habitat use and prey selection by Yuma bats, *Myotis yumanensis*. J. Mammal. 73(3):640-645.
- CLARK, D. R., JR., R. K. LAVAL, M. D. TUTTLE. 1982. Estimating pesticide burdens of bats from guano analysis.Bull.Environm.Contam.Toxicol.29:214-220.
- COCKRUM, E. L. 1969. Migration in the guano bat, *Tadarida brasiliensis*. Univ. Kans. Mus. Natur. Hist. Misc.Public.52:303-336.
- ------. 1991. Seasonal distribution of northwestern populations of the long-nosed bats, *Leptonycteris sanborni*, family *Phyllostomidae*. Anales Inst. Biol. Nac. Autón. †Mexico, Ser. Zool. 62(2): 181-202.
- AND E. ORDWAY. 1959. Bats of the Chiricahua Mountains, Cochise County, Arizona. Am. Mus. Novitates 1938.35pp.
- AND Y. PETRYSZYN. †1991. †The long-nosed bat, *Leptonycteris*: an endangered species in the southwest? †Occ. Papers The Mus. Texas Tech Univ. 142:1-32.
- ——— AND ——. n.d. Tree bats of Arizona. (unpubl. manuscript.)
- CORDES, B. 1994. Pentachlorophenol burden in the greater mouse-eared bat *Myotis myotis* from northern Bavaria.Bat Res.News 35(1):19.
- COX, P. A., T. ELMQVIST, E. D. PIERSON, W. E. RAINEY. 1991. Flying foxes as strong interactors in South Pacific island ecosystems: a conservation hypothesis. Cons. Biol.5(4):448-454.
- DALTON, V. M., V. BRACK, JR., P. M. MCTEER. 1986. Food habits of the big-eared bat, *Plecotus townsendii virginianus*, in Virginia. Va. J. of Science 37(4):248-254.
- ------, V. W. BRACK, JR., C. WILLIAMS. 1989. Foraging ecology of the Virginia big-eared bat. Pages 32-46 in: Virginia Nongame and Endangered Wildlife Investi-

gations, Ann. Rep. Virg. Dept. of Game and Inland Fisheries.

- ——— AND D. C. DALTON. 1993. Assessment of the impacts of low level military aircraft on *Leptonycteris curasoae*, an endangered bat [...]. Final report for USAF/ Luke AFB, AZ 85309, Contract No. F0260492MS359.iii+54pp.
- AND ———. 1994a. Census protocol for the longnosed bat (*Leptonycteris curasoae*) [...]. For Organ Pipe Cactus Nat.Mon., Ajo, AZ 85321.20pp.
- AND ———. 1994b. Roosting and foraging use of proposed mine expansion sites by the long-nosed bat (*Leptonycteris curasoae*) and the California leaf-nosed bat (*Macrotus californicus*). For Cyprus Casa Grande Corp., Casa Grande, AZ 85230.28pp.
- FENTON, M. B. 1982. Echolocation, insect hearing, and feeding ecology of insectivorous bats. Pages 261-286 *in* T. H. Kunz, ed. Ecology of Bats. Plenum Press, New York.
- FLEMING, T. H. 1982. Foraging strategies of plant-visiting bats. Pages 287-326 *in* T. H. Kunz, ed. Ecology of Bats. Plenum Press, New York.
- ———, R. A. NUÑEZ, L. STERNBERG. 1993. Seasonal changes in the diets of migrant and non-migrant nectarivorous bats as revealed by carbon stable isotope analysis. Oecologia 94:72-75.
- GAISLER, J. 1979. Ecology of bats. Pages 281-342 *in* D. M. Stoddart, ed. Ecology of small mammals. Chapman and Hall, London.
- GARDNER, A. L. 1977. Feeding habits. Pages 293-350 in Baker, R. J., J. K. Jones, Jr., D. C. Carter, eds. Biology of Bats of the New World Family Phyllostomatidae (II). The Museum, Special Publ. No.13. Texas Tech Press, Lubbock, Texas.
- HERD, R. M. AND M. B. FENTON. 1983. An electrophoretic, morphological, and ecological investigatoin of a putative hybrid zone between *Myotis lucifugus* and *Myotis yumanensis* (Chiroptera: Vestpertilionidae).Can.J.Zool.61(9):2029-2050.
- HOFFMEISTER, D. F. 1970. The seasonal distribution of bats in Arizona: a case for improving mammalian range maps.Southwestern Naturalist 15(1):11-22.
- HOWELL, D. J. AND B.S. ROTH. +1981. Sexual reproduction in agaves: the benefits of bats; the cost of semelparous advertising. Ecol. 62(1):1-7.
- JANOVY, J., JR. 1985. On Becoming a Biologist. Harper and Row, N.Y. xii + 160pp.
- JONES, J.K., JR., R.S. HOFFMANN, D.W. RICE, C. JONES, R. J. BAKER, M. D. ENGSTROM. 1992. Revised checklist of North American mammals north of Mexico, 1991. Occas. Papers Mus. (146), Texas Tech Univ. 23pp...
- KUNZ, T. H. 1982. Roosting ecology of bats. Pages 1-55 in T. H. Kunz, ed. Ecology of Bats. Plenum Press, New York.

-----, ed. 1988. Ecological and Behavioral Methods for the Study of Bats. Smithsonian Inst. Press, Wash. D.C. xxii + 533.

———. AND A. KURTA. 1988. Capture methods and holding devices. Pages 1-30 *in* T. H. Kunz, ed. Ecological and Behavioral Methods for the Study of Bats. Smithsonian Inst. Press, Wash. D.C.

- LEE, D. L. AND M. K. CLARK. 1993. Arizona's night visitors. Bats 11(2):3-5.
- LOWE, C.H. ANDD. E. BROWN. 1973. The natural vegetation of Arizona. Az. Res. Info. Sys., No. 2.53pp.
- MCCRACKEN, G.F., M.K. MCCRACKEN, A.T. VAWTER. 1994. Genetic structure in migratory populations of the bat *Tadarida brasiliensis mexicana*. J. Mammal. 75(2):500-514.
- MOHR, C. E. 1972. The status of threatened species of cave-dwelling bats. Bull.Nat.Speleol.Soc. 34(2):33-47.
- NEUWEILER, G. 1984. Foraging, echolocation and audition in bats. Naturwiss. 71:446-455.
- ORR, R. T. 1970. Development: prenatal and postnatal. Pages 217-232 *in* W. A. Wimsatt, ed. Biology of Bats (I). Academic Press, New York.
- PARSONS, H.J., D.A. SMITH, ANDR.F. WHITTAM. 1986. Maternity colonies of silver-haired bats, *Lasionycteris noctivagans*, in Ontario and Saskatchewan. J. Mamm. 67:598-600.
- PEARSON, O. P., M. R. Koford, A. K. Pearson. 1952. Reproduction of the lump-nosed bat (*Corynorhinus rafinesquei*) in California. J. Mammal. 33(3):273-320.
- PIERSON, E. D. AND G. M. FELLERS. 1993. Injuries to *Plecotus townsendii* from lipped wing bands. Bat. Res. News 34(4):89-91.
  - ------, W. E. RAINEY, D. M. KOONTZ. 1991. Bats and mines: experimental mitigaton for Townsend's bigeared bat at the McLaughlin mine in California. Pages 31-42 *in* Proc. Thorne Ecological Institute. Issues and Technology in Management of Impacted Wildlife, April 8-10, 1991. Snowmass, Colorado.
- RAINEY, W. E., E. D. PIERSON, M. COLBERG, and J. H. BARCLAY. 1992. Bats in hollow redwoods: seasonal use and role in nutrient transfer into old growth communities. Bat. Res. News 33(4):71.
  - J.SIPEREK, R.M. MILLER. (In press) First report of colonial maternity roosts of the silver-haired bat (*Lasionycteris noctivagans*) in the United States. American Midland Naturalist.<sup>+</sup>
- REIDINGER, R. F., JR. 1972. Factors influencing Arizona bat population levels. Ph.D. Diss. Univ. Arizona, Tucson.xiii+172.
- RICHTER, A. R., S. R. HUMPHREY, J. B. COPE, V. BRACK, JR. 1993. Modified cave entrances: thermal effect on body mass and resulting decline of endangered Indiana bats (*Myotis sodalis*). Cons. Biol.7(2):407-415.

- SAUGEY, D. A. 1991. U. S. National forests: unsung home to American's bats.Bats9(3):3-6.
- SHEFFIELD, S. R., J. H. SHAW, G. A. HEIDT, L. R. MCCLE-NAGHAN. 1992. Guidelines for the protection of bat roosts. J. Mammal. 73(3):707-710.
- STEBBINGS, R. E. 1966. Bats under stress. Studies in Speleology 1(4):168-173.
- STEPHENSON, A. G. 1984. The regulation of maternal investment in an indeterminate flowering plant (*Lotus corniculatus*). Ecology 65:114-121.
- SUTHERLAND, S. 1986. Floral sex ratios, fruit-set, and resource allocation in plants. Ecology 67(4): 991-1001.
- ——. 1987. Why hermaphroditic plants produce many more flowers than fruits: experimental tests with Agave mckelveyana. Evolution 41(4):750-759.
- ---------. ANDL.F.DELPH.1984.On the importance of male fitness in plants: patterns of fruit-set. Ecology 65(4):1093-1104.
- THOMAS, D. W. 1988. Analysis of diets of plant-visiting bats. Pages 211-220 *in* T. H. Kunz, ed. Ecological and Behavioral Methods for the Study of Bats. Smithsonian Inst. Press, Wash. D.C.
- -------, G. P. BELL, M. B. FENTON. 1987. Variation in echolocation call frequencies recorded from North American vespertilionid bats: a cautionary note. J. Mammal.68(4):842-847.
- ———— AND R. K. LAVAL. 1988. Survey and census methods. Pages 77-89 *in* T.H. Kunz, ed. Ecological and behavioral methods for the study of bats. Smithsonian Institution Press, Wash.D.C.
- ——— AND S. D. WEST. 1991. Forest age associations of bats in the Southern Washington Cascade and Oregon Coast Ranges. Pages 295-303 *in* Wildlife and Vegetation of Unmanaged Douglas-Fir Forests. US For. Serv. Gen. Tech. Rep. PNW 0(285).
- TIPTON, V.M. 1984. Evidence of movement of a maternity colony of *Plecotus townsendii virginianus* throughout the summer. Va. J. Sci. 35(2):90.
- UDOVIC, D. 1981. Determinants of fruit set in *Yucca whipplei*: reproductive expenditure vs. pollinator availability. Oecologia (Berl) 48:389-399.
- WILKINSON, G. S. AND J. W. BRADBURY. 1988. Radiotelemetry: techniques and analysis. Pages 105-124 *in* T. H. Kunz, ed. Ecological and Behavioral Methods for the Study of Bats. Smithsonian Inst. Press, Wash. D.C.
- WHITAKER, J. O., JR. 1988. Food habits analysis of insectivorous bats. Pages 171-190 in T. H. Kunz, ed. Ecological and Behavioral Methods for the Study of Bats.Smithsonian Inst. Press, Wash. D.C.