# RESOURCE AND SPATIAL-USE PATTERNS OF AN ENDANGERED VERTEBRATE POLLINATOR, THE LESSER LONG-NOSED BAT

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*Abstract:* Understanding how the distribution and abundance of food resources influence space use of organisms is an important element of successful conservation and recovery strategies for endangered species. We investigated interrelationships between space use, activity patterns, and food resources for lesser long-nosed bats (*Leptonycteris curasoae*), an endangered nectar-feeding bat, during an energetically demanding phase of its annual life cycle. We estimated the size of home ranges (95% kernel areas) and core use-areas (50% kernel areas) of bats and estimated density of their forage plant (*Agave palmeri*) in and near these use areas. Density ($\bar{x} \pm$ SE plants/ha) of flowering agaves within home ranges ($3.6 \pm 1.04$) exceeded that which was available on the landscape ($1.8 \pm 0.36$), indicating that bats selected areas with high food abundance. Although density of agaves within home ranges of bats differed in successive years (1998: $3.6 \pm 1.04$; 1999: $0.8 \pm 0.15$), sizes of home ranges and core use-areas of adult bats were similar between years, suggesting that the relationship between home-range size and density of food resources was mediated by other factors. Differences in activity budgets of bats between years suggest that bats altered their behavior in response to changes in food abundance, allocating more time to foraging the year fewer flowering plants were present. Consequently, reductions in agave density could increase energy demands of foraging bats and reduce the chances of successful recovery of lesser long-nosed bat populations.

The quantity and quality of plants as resources for animals varies over space and time (Hunter et al. 1992). This variation in plant distribution and abundance influences the distribution and abundance of animals that rely on these plants. Because flighted animals are highly mobile, they can locate isolated patches of resources and select patches that offer high energetic rewards. Because flight entails a high energetic cost, however, these animals must obtain large quantities of food by either visiting many plants or by efficiently locating plants with high energy rewards (Heinrich 1975).

To be available to an organism, food resources must be located nearby other required resources such as nesting or roosting sites. Therefore, both the abundance and spatial arrangement of potentially limiting resources should be considered when planning conservation and recovery strategies for rare species. For example, roost sites and food resources are resources required for all bats (Kunz and Lumsden 2003). Bats that roost in permanent structures, such as caves and mines, tend to be site faithful (Lewis 1995). Protecting these resources is relatively simple compared to protecting food resources that are often

ephemeral. Consequently, conservation efforts for bats typically provide detailed plans for the protection of roost structures but neglect strategies for protecting food resources. Understanding interrelationships between foraging areas and roost sites will increase the efficacy of conservation plans for bats.

The distribution and migratory routes of lesser long-nosed bats coincide with the distribution and phenology of the cacti and agaves whose nectar, pollen, and fruit they consume (Gentry 1982, Fleming et al. 1993). Individuals that migrate to southern Arizona represent the northern-most populations of the species. Diets of individuals that inhabit southeastern Arizona in late summer consist primarily of nectar and pollen from a single species of agave, *Agave palmeri* (Beatty 1955, Hayward and Cockrum 1971, Howell 1972, Hevly 1979). As foragers, bats are influenced by the distribution of flowering plants, and as pollinators, bats influence the future distribution of agaves (Heithaus et al. 1975, Schaffer and Schaffer 1979).

Lesser long-nosed bats were listed as endangered in the United States in 1988 (Shull 1988, USFWS 1995). To adequately understand the relationships among food resources, roost sites, and bat movements, we assessed how spatial variability in resource abundance affected habitat use and foraging behavior of bats. Specifically, we

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assessed (1) size of home ranges and core use-areas of bats; (2) location of home ranges and core use-areas in relation to day roosts, night roosts, and use-areas of other bats; (3) density and distribution of nectar-producing agaves within home ranges and across the landscape; and (4) whether spatial-use patterns and activity budgets of bats varied with distribution and abundance of agaves.

## METHODS

### Study Area

Our study took place in southeastern Arizona, USA (31°30′N, 110°20′W) in an area defined by the Patagonia Mountains to the west, the Mustang Mountains to the north, the Huachuca Mountains to the east, and Mexico to the south. Elevation varied from 1,400 m in the lowest grasslands to 2,885 m in the surrounding mountains. This region typically receives bimodal precipitation, with substantial rainfall in summer and winter. Annual precipitation in the area averages 391 mm, with 88 mm falling in August and 44 mm in September (Sellers et al. 1985). Daily minimum and maximum temperatures average 17.4°C and 30.7°C in August and 15.4°C and 29.2°C in September (Sellers et al. 1985).

Vegetation below 1,600 m was semidesert grassland, characterized by perennial grass–scrub, and at higher elevations vegetation was Madrean evergreen woodland, characterized by oak (*Quercus arizonica*), juniper (*Juniperus deppeana*), and pinyon (*Pinus cembroides*) (Brown 1982). *Agave palmeri* was 1 of 2 species of chiropterophilous agave in the family Ditepelae in this region; the other (*Agave parryi*) was rare (<0.1% of agaves in the study area) and was not considered. *A. palmeri* was widely scattered in disjunct patches between 930 and 1,850 m elevation, primarily on xeric sites with rocky soils (Gentry 1982).

### Bat Movements

We used radiotelemetry to investigate nocturnal movements and activity patterns of lesser long-nosed bats during August and September 1998 and 1999. This period is an energetically demanding phase in the species' annual cycle because it precedes the bats' southward migration in late September.

Each year we captured 30 individuals at a single night roost and we determined sex, age, body mass, and reproductive status for each. We then trimmed fur from the bats' upper backs and affixed transmitters (model BD-2A and model BD-2, Holohil Systems, Ltd.) with Skinbond medical adhesive. On average, transmitters weighed 0.86 g (3.5% of body mass) and had life expectancies of 3–6 weeks. The study protocol was approved by the University of Arizona Animal Care and Use Committee.

We monitored movements of bats from a network of tracking stations located on hilltops throughout the study area. At each tracking station, we secured a 3- or 5-element Yagi antenna atop a 2-m mast to increase the range of detection (Mech 1983). Each mast supported a compass aligned exactly with the main axis of the antenna to increase the accuracy of bearings. Field personnel (4–7 individuals) equipped with a receiver scanned all frequencies sequentially from sunset to sunrise. When an observer detected a bat, they notified others via radio and bearings were recorded simultaneously on the minute throughout a 3-min period before scanning other frequencies.

When locations were estimated from ≥3 simultaneous bearings, we used Lenth's (1981) maximum likelihood estimator (Nams 1996). We determined accuracy of bearings by placing reference transmitters in several locations unknown to field personnel and compared estimates to true locations. Standard deviations of diversions of bearings were pooled to derive a mean standard deviation ($\bar{x} = 5°$) that we used to calculate error ellipses for all locations generated from ≥3 simultaneous bearings (White and Garrott 1990). We only included 2-bearing fixes when locations were near (<10 km) observers and near (<2 km) previous and subsequent locations.

Because lesser long-nosed bats can traverse their home range in a few minutes, we used 5 min as the minimum time between successive locations of active individuals (White and Garrott 1990, Otis and White 1999). Estimates of home ranges and core use-areas using longer periods between successive locations were virtually identical to those using locations taken 5 min apart, suggesting that locations taken 5 min apart were not autocorrelated (Ober 2000).

We quantified bat use of the landscape at 2 spatial scales. At the coarser scale, we estimated home ranges that we defined as the smallest area containing 95% of all locations for each animal based on locations with error polygons <1,600 ha. At a finer scale that represented areas bats used frequently, we estimated core use-areas that we defined as the smallest area containing 50% of all

locations for each animal based on only those fixes generated from ≥3 simultaneous bearings with error polygons <200 ha. We calculated sizes of home ranges and core use-areas using cross-validated, fixed-kernel methods (Worton 1989, Kenward and Hodder 1996) because they provide range size estimates with little bias and low error (Worton 1995, Seaman and Powell 1996), and because they competently highlight areas of concentrated activity (Worton 1987). We also used fixed-kernel methods to estimate the extent of overlap between individual home ranges and core use-areas of bats that we tracked concurrently.

We assessed the location of home ranges and core use-areas in relation to day and night roosts for each bat with known roost locations. We computed the distance between day roosts and the geometric center of core use-areas (commute distance, Hayne 1949) as well as distances between night roosts and the geometric center of core use-areas.

### Resource Abundance

*A. palmeri* was the dominant structural element in the open grasslands we studied. A monocarpic succulent that takes several decades to mature, each flowering agave produces a single inflorescence that can grow up to 7 m and can remain standing for several years after flowering (Howell and Roth 1981). We estimated density of flowering agaves to assess food abundance for bats and density of dead-standing agave inflorescences to gauge previous levels of food abundance. We also calculated densities of live and dead-standing inflorescences combined, as density of all standing agave inflorescences may function as a visual cue to resource abundance for bats. We estimated densities using variable-width line transects (Buckland et al. 1993) established within home ranges in both years and landscape-wide in 1998. We measured distances from the transect to agaves along 77.6 km of transects within and adjacent to bat home ranges in 1998 and along 39.5 km of transects within bat home ranges in 1999.

### Bat Activity Patterns

We measured time-activity budgets of a subset of radiomarked bats and classified their behaviors into 4 activities: day roosting, commuting, night roosting, and foraging. We estimated time spent day roosting by calculating the average time of emergence from and reentry to day roosts by radiomarked individuals on 11 nights. We calculated average flight speeds by dividing the mean

distance between day roosts and geometric centers of core use-areas by the mean time bats spent flying between day roosts and core use-areas, and we then divided the mean of all known commute distances by mean flight speeds to arrive at an estimate of mean time spent commuting. We estimated time spent foraging and night roosting by tracking single bats continuously from emergence to reentry to day roosts. We determined time spent resting between foraging bouts by noting a constant radio signal indicating no movement, and we added this to time spent in caves and mines during the night to determine total time spent night roosting. We estimated time spent night roosting by averaging the time not day roosting or commuting that was spent resting. Remaining time was classified as foraging.

### Statistical Analyses

We compared commute distances, sizes of home ranges and core use-areas, densities of flowering and dead-standing agave inflorescences within home ranges, and time spent day roosting and commuting between bats monitored in different years and between bats of different ages using 2-sample *t*-tests. Data were square-root, reciprocal, or natural-log transformed when necessary to meet assumptions of parametric tests; we reported means and standard errors on the original scale of measurement. If we failed to detect a difference between groups, we calculated retrospective power (and the 90% confidence interval for power) to detect a 20% difference between groups for $\alpha = 0.10$ (Steidl and Thomas 2001). We used multiple regression to assess relationships between home-range sizes of bats and densities of live, dead-standing, or live and dead-standing agaves, after adjusting for potential effects of year and number of nights a bat was tracked.

### RESULTS

In 1998, we tracked 28 adult and 2 juvenile female bats for 1 to 15 nights ($\bar{x} = 4.3$, SE = 0.70); we tracked 19 of these individuals for ≥3 nights. In 1999, we tracked 25 adult and 5 juvenile females for 1 to 17 nights ($\bar{x} = 7.6$, SE = 0.54); we tracked 26 of these individuals for ≥3 nights. We collected 50,792 bearings during 2,650 person-hours of tracking.

### Bat Movements

Although we captured all radiomarked bats at the same night roost, individuals used different day roosts. The 3 day roosts used by most bats (*n*

Table 1. Home-range sizes (95% kernel) of lesser long-nosed bats, southeastern Arizona, USA, 1998 and 1999.

| Year | Age | n | No. locations | | | Home-range size (ha) | | |
|---|---|---|---|---|---|---|---|---|
| | | | $\bar{x}$ | SE | Range | $\bar{x}$ | SE | Range |
| 1998 | Adult | 4 | 84 | 22 | 29–138 | 2,247 | 512 | 755–3,083 |
| 1999 | Adult | 17 | 59 | 8 | 11–131 | 1,903 | 377 | 119–5,166 |
| 1999 | Juvenile | 4 | 64 | 13 | 30–90 | 1,740 | 586 | 590–3,336 |
| Overall | All | 25 | 64 | 7 | 11–138 | 1,932 | 278 | 119–5,166 |

= 37 of 60) were 17, 20, and 27 km from the night roost and 28, 41, and 43 km from one another. In 1998, all bats were faithful to a single day roost each during sampling, whereas in 1999, 27% of bats switched from use of 1 day roost to another.

Straight-line distance from day roosts to core use-areas (commute distance) averaged 19.2 km (SE = 1.29, $n$ = 22), was similar between years for adult bats ($t_{16}$ = 0.67, $P$ = 0.51; power = 0.26, 90% C.I. = 0.18–0.35), and was similar between juveniles and adults in 1999 ($t_{16}$ = 0.21, $P$ = 0.84; power = 0.37, 90% C.I. = 0.24–0.52). Permanent night roost structures (2 mines and 1 natural alcove) were located an average of 2.0 km (SE = 0.45, $n$ = 4) from the center of core use-areas.

Home-range sizes ranged widely, from 119 to 5,166 ha (Table 1). For adults, home-range sizes were similar between years ($t_{19}$ = 0.80, $P$ = 0.43; power = 0.83, 90% C.I. = 0.60–0.95). Home-range sizes of adults and juveniles in 1999 were also similar ($t_{19}$ = 0.20, $P$ = 0.84; power = 0.83, 90% C.I. = 0.60–0.95).

Core use-areas ranged in size from 1 to 92 ha (Table 2). For adults, sizes of core use-areas were similar between years ($t_{19}$ = 0.55, $P$ = 0.59; power = 0.21, 90% C.I. = 0.16–0.27). Size of core use-areas

for adults and juveniles in 1999 were also similar ($t_{19}$ = 1.02, $P$ = 0.32; power = 0.23, 90% C.I. = 0.17–0.30).

Although bats used day roosts located as much as 43 km from one another, they foraged in areas that overlapped. When considering every possible pair of bats tracked concurrently, 63% of home-range pairs in 1999 (63 of 100) overlapped; of those that did, overlap averaged 35% (SE = 2.8%). In contrast, only 5% of core use-area pairs in 1999 (5 of 100) overlapped; of those that did, overlap averaged 31% (SE = 9.9%). The maximum extent of overlap between home ranges of bats tracked simultaneously was 100%, and between core use-areas it was 88%.

## Resource Abundance

In home ranges of adult bats, density of flowering agaves was >4 times higher in 1998 than in 1999 ($t_{19}$ = 5.05, $P$ < 0.0001), whereas density of dead-standing agave inflorescences was similar between years ($t_{19}$ = 0.04, $P$ = 0.97; Table 3). Density of live and dead-standing agave inflorescences combined in home ranges of adults averaged 2.8 (SE = 1.10) plants/ha greater in 1998 than in 1999 ($t_{19}$ = 2.58, $P$ = 0.02; Table 3).

In 1998, density (plants/ha) of flowering agaves (3.6 ± 1.04) in home ranges of adults was twice that available on the landscape (1.8 ± 0.36; $t_{92}$ = 2.41, $P$ = 0.009), and density of dead-standing inflorescences (3.5 ± 0.54) was >4 times that available on the landscape (0.8 ± 0.17; $t_{78}$ = 3.83, $P$ = 0.0001). In 1999, densities of flowering agaves, dead-standing agaves, and both combined were similar within home ranges of adults and juveniles ($P \geq$ 0.53, Table 3).

Home-range size did not vary appreciably with density of flowering agaves ($t_{19}$ = 0.14, $P$ = 0.89) or with density of live and dead-standing agave inflorescences combined ($t_{19}$ = 1.31, $P$ = 0.21) for adults (Fig. 1).
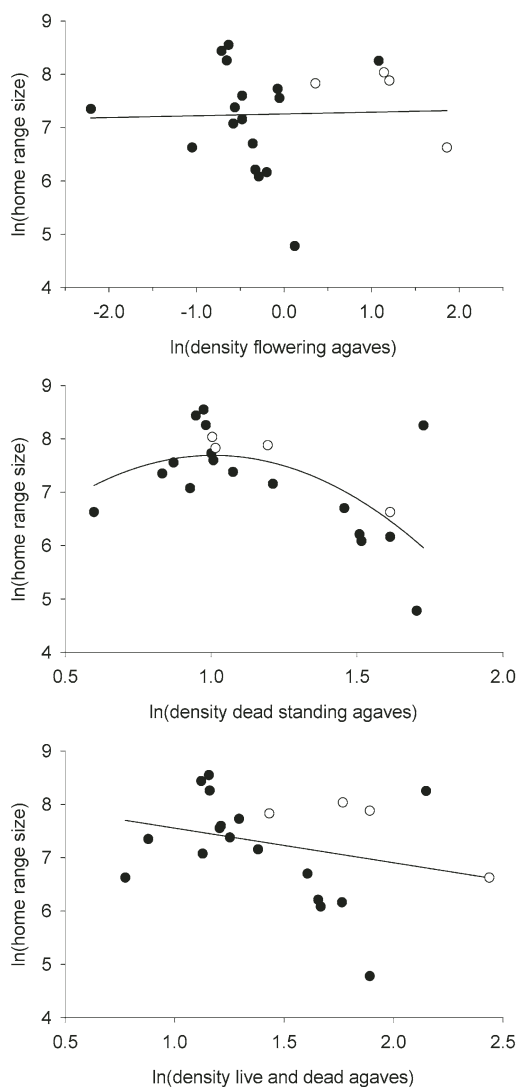
Table 2. Core use-area sizes (50% kernel) of lesser long-nosed bats, southeastern Arizona, USA, 1998 and 1999.

| Year | Age | n | No. locations | | | Core use-area size (ha) | | |
|---|---|---|---|---|---|---|---|---|
| | | | $\bar{x}$ | SE | Range | $\bar{x}$ | SE | Range |
| 1998 | Adult | 4 | 14 | 5.0 | 4–27 | 33 | 20.1 | 6–92 |
| 1999 | Adult | 17 | 38 | 6.2 | 6–94 | 22 | 5.1 | 1–73 |
| 1999 | Juvenile | 4 | 48 | 10.6 | 20–68 | 26 | 4.5 | 16–37 |
| Overall | All | 25 | 36 | 4.9 | 4–94 | 24 | 4.6 | 1–92 |

Table 3. Densities (plants/ha) of flowering *A. palmeri*, dead standing *A. palmeri*, and both combined within home ranges of lesser long-nosed bats, southeastern Arizona, USA, 1998 and 1999.

| Year | Age | Density of *A. palmeri* | | | | | |
|---|---|---|---|---|---|---|---|
| | | Flowering | | Dead standing | | Flowering and dead standing combined | |
| | | $\bar{x}$ | SE | $\bar{x}$ | SE | $\bar{x}$ | SE |
| 1998 | Adult | 3.6 | 1.04 | 3.5 | 0.54 | 7.0 | 1.56 |
| 1999 | Adult | 0.8 | 0.15 | 3.4 | 0.30 | 4.2 | 0.41 |
| 1999 | Juvenile | 0.7 | 0.12 | 3.0 | 0.07 | 3.7 | 0.16 |

Table 4. Daily activity budgets for lesser long-nosed bats (hrs engaged in each activity per night), southeastern Arizona, USA, 1998 and 1999.

| | Year | | | |
|---|---|---|---|---|
| | 1998 | | 1999 | |
| Behavior | $\bar{x}$ | SE | $\bar{x}$ | SE |
| Day roosting | 16.8 | 0.28 | 16.5 | 0.27 |
| Commuting | 1.0 | 0.18 | 1.1 | 0.08 |
| Night roosting | 3.9 | 0.31 | 1.3 | 0.34 |
| Foraging | 2.3 | 0.44 | 5.1 | 0.49 |

Fig. 1. Home-range size (ha) of adult lesser long-nosed bats versus density of flowering *A. palmeri*, density of dead standing *A. palmeri*, and density of both combined (plants/ha) in southeastern Arizona, USA. Closed circles represent 1999 data, open circles represent 1998 data.

However, home-range size decreased with increasing density of dead-standing agave inflorescences (linear term: $t_{18} = 1.1$, $P = 0.059$; quadratic term: $t_{18} = 1.81$, $P = 0.087$) for adult bats in 1999 (Fig. 1). Home-range size did not vary with either year ($P > 0.18$, for all analyses) or number of nights we tracked a bat ($P > 0.66$, for all analyses).

## Bat Activity Patterns

The ways bats allocated their time to foraging and resting while away from the day roost varied greatly between years (Table 4), although bats spent approximately the same amount of time day roosting ($16.6 \pm 0.20$ hrs for 1998 and 1999 combined) and commuting ($1.1 \pm 0.07$ hrs for 1998 and 1999 combined) in 1998 and 1999 ($P > 0.35$). In 1998, 37% (2.3 hrs) of the time bats spent away from day roosts but not commuting was spent foraging, and 63% (3.9 hrs) was spent resting, compared to 1999 when 80% (5.1 hrs) of this time was spent foraging and 20% (1.3 hrs) was spent resting.

## DISCUSSION

Availability of agave nectar varies spatially and temporally, which in turn influences the behavior of nectar-feeding bats. Individual *A. palmeri* flowers produce nectar for 5 consecutive nights before wilting, and each plant may produce 1,600–2,240 flowers during a single flowering season (Slauson 1999) that spans approximately 40 days (Howell and Roth 1981). This, coupled with asynchronous flowering among agaves within a population, results in a spatial distribution of nectar that changes over the course of several weeks but not over the course of several days. This flowering pattern likely explains why we observed bats returning to the same areas on consecutive nights, a pattern reported for lesser long-nosed bats in Sonora, Mexico (Horner et al. 1998), and for other nectarivorous (Lemke 1984) and frugivorous bats (Heithaus and Fleming 1978). Because areas rich in food resources 1 night are likely to be rich the following night, bats eliminated the energy expenditure that searching for new plants would require by returning to the same area on subsequent nights.

Because mobile animals are able to sample food from a large area, systematic changes in space use likely reflect changes in local food abundance. The abrupt switch of several bats from 1 core use-area to another coincided with the cessation of nectar production from agaves in the original area (H. Ober, University of Arizona, personal observation). Once an area was aban-

doned, bats did not return. Fidelity to day roosts may also be associated with changes in food abundance. No radiomarked bats switched day roosts during the summer when food abundance was high, but several did switch during the summer when resources were scarcer, suggesting that bats may abandon day roosts when food becomes limited nearby.

Density of flowering and dead-standing agaves in home ranges of adults was greater than that available on the landscape, suggesting that bats selected areas with high food abundance and evidence of high food abundance in previous years. However, sizes of home ranges and core use-areas did not vary between years, despite a large difference in density of flowering agaves, nor did home-range sizes vary with density of flowering agaves (Fig. 1). Because home-range size of bats was relatively consistent despite variation in food abundance, we suggest that bats compensated for reduced food abundance by changing their activity patterns rather than by altering home-range size.

When few plants flower, average distance between flowering plants is farther than when many plants flower, so bats must spend more time foraging and less time resting. Moreover, a greater number of bats may need to feed at each plant, potentially reducing resources on a local scale. Bats spent an average of 120% more time foraging and 66% less time night roosting the year food resources were lower than they had the year food resources were more plentiful, suggesting that bats experienced increased energetic demands the year food abundance was relatively low. Small differences in activity budgets can alter energy requirements of bats drastically (Ober 2000). Increased energetic demands can be particularly challenging to species preparing for migration due to the elevated energy expenditure required during extended periods of continuous flight (Berger and Hart 1983).

Overlap in home ranges and core-use areas among bats suggest that lesser long-nosed bats are not territorial, unlike other nectarivorous bats, such as *Glossophaga soricina* (Lemke 1984). Individuals that were captured night roosting together also fed in the same areas simultaneously, yet they used day roosts located far from one another. Although areas with densities of flowering agaves as high as 9.9 plants/ha existed in the study area, bats returned repeatedly to the area near the night roost where they were captured. This suggests that in addition to the density of flowering agaves, site fidelity and proximity to

suitable night roosts likely influenced habitat suitability for lesser long-nosed bats.

Bats commuted from day roosts to foraging areas an average, straight-line distance of 18.9 km; this distance is relatively long in comparison to most bat species but somewhat less than has been reported for lesser long-nosed bats elsewhere. For example, in Sonora, Mexico, lesser long-nosed bats commuted an average of 27.2 km (Sahley et al. 1993). Scarcity of appropriate day roosts likely explains the bats' long commute distances. In our study, bats flew commute distances up to 28.2 km to forage, despite the presence of food resources much closer to roosts; perhaps they flew this extra distance to avoid competition for nectar at plants nearer the roost (Ober and Steidl 2004). Long-distance commuting may not be a serious constraint for bats of the genus *Leptonycteris*, however, because they have high wing loading and the greatest mass of all bats in the subfamily Glossophaginae (Sahley et al. 1993), and these attributes combine to reduce the energy cost of transport and to increase flight speed (Brown et al. 1978, Norberg and Rayner 1987).

## MANAGEMENT IMPLICATIONS

Both abundance of food resources and presence of night roosts were important determinants of space use for lesser long-nosed bats, suggesting that both of these resources—as well as their spatial arrangement—need to be considered when developing management strategies for this endangered species. The high variability in the number of flowering *A. palmeri* on the landscape from one year to the next (Nobel 1988, Ober 2000) may lead to previously unrecognized differences in energy expenditures by bats, such as we observed in the 2 years of this study.

With the seasonal influx of an estimated 70,000 lesser long-nosed bats (Fleming et al. 2003), the density of food plants required to support bat populations in this region is considerable and may be limiting in years when few agaves flower. Reductions in numbers of flowering *A. palmeri*, therefore, could increase energy demands on bats, forcing them to commute farther, to roost in substandard roosts, or to compete more for food at remaining plants, all of which could have adverse consequences for this bat population.

We recommend that the density of flowering agaves be monitored annually in areas that support bat populations so that in years when flowering is at or below 1.8 flowering agaves per hectare (landscape-wide estimate in 1998), human uses of these

mid-elevation grasslands that could compromise the chances of successful flowering (Widmer 2002) be curtailed until flowering has been completed.

## ACKNOWLEDGMENTS

## LITERATURE CITED

BEATTY, L. D. 1955. Autoecology of the long-nosed bat, *Leptonycteris nivalis* (Saussure). Thesis, University of Arizona, Tucson, USA.

BERGER, M., AND J. S. HART. 1983. Physiology and energetics of flight. Pages 415–477 *in* D. Farner and J. R. King, editors. Avian biology. Volume VII. Academic Press, New York, USA.

BROWN, D. E. 1982. Biotic communities of the American southwest—United States and Mexico. Desert Plants 4:1–342.

BROWN, J. H., W. A. CALDER, AND A. KODRIC-BROWN. 1978. Correlates and consequences of body size in nectar-feeding birds. American Zoologist 42:687–700.

BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, AND J. L. LAAKE. 1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall, New York, USA.

FLEMING, T. H., R. A. NUNEZ, AND L. S. 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.

———, T. TIBBITTS, Y. PETRYSZYN, AND V. DALTON. 2003. Current status of pollinating bats in southwestern North America. Pages 63–68 *in* T. J. O'Shea and M. A. Bogan, editors. Monitoring trends in bat populations of the United States and territories: problems and prospects. Information and Technology Report USGS/BRD/ITR-2003-0003. U.S. Geological Survey, Fort Collins, Colorado, USA.

GENTRY, H. S. 1982. Agaves of continental North America. University of Arizona Press, Tucson, USA.

HAYNE, D. W. 1949. Calculation of size of home range. Journal of Mammalogy 30:1–18.

HAYWARD, B., AND E. L. COCKRUM. 1971. The natural history of the western long-nosed bat, *Leptonycteris sanborni*. Western New Mexico University, Research Sciences 1:75–123.

HEINRICH, B. 1975. Energetics of pollination. Annual Review of Ecology and Systematics 6:139–170.

HEITHAUS, E. R., AND T. H. FLEMING. 1978. Foraging movements of a frugivorous bat, *Carollia perspicillata* (Phyllostomatidae). Ecological Monographs 48:127–143.

———, ———, AND P. A. OPLER. 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. Ecology 56:841–854.

HEVLY, R. H. 1979. Dietary habits of two nectar and pollen feeding bats in southern Arizona and northern Mexico. Journal of the Arizona–Nevada Academy of Science 14:13–18.

HORNER, M. A., T. H. FLEMING, AND C. T. SAHLEY. 1998. Foraging behavior and energetics of a nectar-feeding bat, *Leptonycteris curasoae* (Chiroptera: Phyllostomidae). Journal of Zoology of London 244:575–586.

HOWELL, D. J. 1972. Physiological adaptations in the syndrome of chiropterophily with emphasis on the bat *Leptonycteris* Lydekker. Dissertation, University of Arizona, Tucson, USA.

———, AND B. S. ROTH. 1981. Sexual reproduction in agaves: the benefits of bats; the cost of semelparous advertising. Ecology 62:1–7.

HUNTER, M. D., T. OHGUSHI, AND P. W. PRICE. 1992. Effects of resource distribution on animal–plant interactions. Academic Press, San Diego, California, USA.

KENWARD, R. E., AND K. H. HODDER. 1996. RANGES V: an analysis system for biological location data. Institute of Terrestrial Ecology, Furzebrook Research Station, Wareham, Dorset, United Kingdom.

KUNZ, T. H., AND L. F. LUMSDEN. 2003. Ecology of cavity and foliage roosting bats. Pages 3–89 *in* T. H. Kunz and M. B. Fenton, editors. Bat ecology. University of Chicago Press, Chicago, Illinois, USA.

LEMKE, T. O. 1984. Foraging ecology of the long-nosed bat, *Glossophaga soricina*, with respect to resource availability. Ecology 65:538–548.

LENTH, R. V. 1981. On finding the source of a signal. Technometrics 23:149–154.

LEWIS, S. E. 1995. Roost fidelity in bats: a review. Journal of Mammalogy 76:481–496.

MECH, L. D. 1983. Handbook of animal radio-tracking. University of Minnesota Press, Minneapolis, USA.

NAMS, V. O. 1996. LOCATE II. Pacer, Truro, Nova Scotia, Canada.

NOBEL, P. S. 1988. Environmental biology of agaves and cacti. Cambridge University Press, New York, USA.

NORBERG, U. M., AND J. M. V. RAYNER. 1987. Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy, and echolocation. Philosophical Transactions of the Royal Society of London 316:355–427.

OBER, H. K. 2000. Foraging ecology of lesser long-nosed bats. Thesis, University of Arizona, Tucson, USA.

———, AND R. J. STEIDL. 2004. Foraging rates of *Leptonycteris curasoae* vary with characteristics of *Agave palmeri*. Southwestern Naturalist 49:68–74.

OTIS, D. L., AND G. C. WHITE. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. Journal of Wildlife Management 63:1039–1044.

SAHLEY, C. T., M. A. HORNER, AND T. H. FLEMING. 1993. Flight speeds and mechanical power outputs of the nectar-feeding bat, *Leptonycteris curasoae* (Phyllostomidae: Glossophaginae). Journal of Mammalogy 74:594–600.

SCHAFFER, W. M., AND M. V. SCHAFFER. 1979. The adaptive significance of variations in reproductive habit in the Agavaceae II: pollinator foraging behavior and selection for increased reproductive expenditure. Ecology 60:1051–1069.

SEAMAN, D. E., AND R. A. POWELL. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

SELLERS, W. D., R. H. HILL, AND M. R. SANDERS. 1985. Arizona climate: the first hundred years. University of Arizona Press, Tucson, USA.

SHULL, A. M. 1988. Endangered and threatened wildlife and plants; determination of endangered status for two long-nosed bats. Federal Register 53:38456–38460.

SLAUSON, L. 1999. Nature of the mutualistic relationship between the Palmer agave and the lesser long-nosed bat. U.S. Department of Agriculture, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

STEIDL, R. J., AND L. THOMAS. 2001. Power analysis and experimental design. Pages 14–36 *in* S. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments, Second edition. Oxford University Press, New York, USA.

USFWS (U.S. FISH AND WILDLIFE SERVICE). 1995. Lesser long-nosed bat recovery plan. U.S. Fish and Wildlife Service, Albuquerque, New Mexico, USA.

WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

WIDMER, K. A. 2002. The relationship between *Agave palmeri* flower stalk herbivory and livestock management in southern Arizona. Thesis, University of Arizona, Tucson, USA.

WORTON, B. J. 1987. A review of models of home range for animal movement. Ecological Modelling 38:277–298.

———. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

———. 1995. Using Monte-Carlo simulation to evaluate kernel-based home range estimators. Journal of Wildlife Management 59:794–800.

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