FORAGING RATES OF *LEPTONYCTERIS CURASOAE* VARY WITH CHARACTERISTICS OF *AGAVE PALMERI*

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ABSTRACT—We examined factors influencing foraging behavior of lesser long-nosed bats, *Leptonycteris curasoae,* in southeastern Arizona. When *L. curasoae* are present in this region, their diet is restricted to nectar and pollen from 1 species, *Agave palmeri,* which has heightened conservation concerns for the plant as forage for this endangered bat. We found that visitation rates of *L. curasoae* to individual *A. palmeri* near a roost were high (mean = 273 ± 17 visits per plant per hour) and varied with the spatial distribution and morphological characteristics of individual plants. Specifically, visitation rates varied with time of night, distance and orientation from the bat roost, and number and relative vertical position of flowers along the inflorescence. We suggest that both spatial distribution and temporal variation in flowering chronology be considered when developing strategies to manage *A. palmeri* to support *L. curasoae.*

RESUMEN—Examinamos los factores que influyen el comportamiento de forrajeo de los murciélagos-hocicudos de Curazao, *Leptonycteris curasoae,* en el sureste de Arizona. Cuando *L. curasoae* está presente en esta región, su alimentación está limitada al néctar y polen de una especie, *Agave palmeri,* lo que ha incrementado las acciones de conservación para la planta de la cual se alimenta este murciélago amenazado. Encontramos que la taza de visita de murciélagos a individuos de *A. palmeri* cerca del dormidero fue alta (promedio = 273 ± 17 visitas por planta por hora) y variaron con la distribución espacial de las plantas y por las características morfológicas de plantas individuales. Específicamente, las tasas de visita estuvieron relacionadas a la hora de la noche, a la distancia y orientación del dormidero, y al número y posición vertical relativa de flores en la inflorescencia. Sugerimos que para el desarrollo de estrategias de manejo de *A. palmeri* con propósitos de conservación de *L. curasoae,* se debe considerar la distribución espacial y la variación en la cronología de afloración.

Bats have high metabolic rates and use an energetically costly form of locomotion (Berger and Hart, 1974). Flight necessitates low body mass, which in turn prevents bats from maintaining large energy reserves (Thomas, 1975). Consequently, homeothermic bats require a constant, relatively energy-rich food supply to meet the extraordinary energy demands imposed by these limitations (von Helversen and Reyer, 1984; Arends et al., 1995). This requires that nectarivorous bats consume large quantities of nectar, which entails visiting many flowers throughout the course of a night (Heinrich, 1975; Neuweiler, 2000).

Lesser long-nosed bats, *Leptonycteris curasoae,* migrate to southeastern Arizona during summer (Cockrum, 1991). Nectar and pollen from a single species of plant, *Agave palmeri,* are the primary foods for these bats in this region (Hayward and Cockrum, 1971; Howell, 1972; Hevly, 1979). *A. palmeri* provides nectar and pollen nocturnally in flowers arranged in umbels on branches spaced widely along a central inflorescence, a nectar production pattern and morphology conducive to pollination by bats (Faegri and Van der Pijl, 1966; Dafni, 1992). *A. palmeri* flower from late June to early October, with peak nectar production between late July and August (Slauson, 2000).

Leptonycteris curasoae is listed as endangered in the United States (Shull, 1988; United States Fish and Wildlife Service, 1995). Although protection of forage plants has been recognized as integral to recovery of the species (United

States Fish and Wildlife Service, 1995), effective conservation strategies have been limited by lack of knowledge of interrelationships between the foraging behavior of bats and their forage plants. To develop effective management and recovery strategies for *L. curasoae,* we must understand how bats select and use forage plants. To determine which characteristics of plants were associated with use by bats, we examined visitation rates of *L. curasoae* to *A. palmeri* near a roost containing 10,000 *L. curasoae* in southern Arizona.

METHODS—*Study Area*—Our study took place in Coronado National Memorial, at the southern end of the Huachuca Mountains, along the border of the United States and Mexico (31°21′N, 110°16′W). Daily maximum and minimum temperatures during August average 31.1°C and 15.8°C, respectively (Sellers et al., 1985). Precipitation between late June and early September consists of frequent, brief, localized thunderstorms in the afternoon or evening.

Vegetation between 1,370 and 1,520 m elevation is desert grassland, characterized by perennial grass-scrub, and at higher elevations is Madrean evergreen woodland, characterized by oaks, juniper, and piñon (Brown, 1982). *A. palmeri* is found in scattered patches between 930 and 1,850 m elevation, primarily in xeric sites with rocky soils (Gentry, 1982). *A. palmeri* comprise only a small percentage of plant biomass at the study site, and the majority of plants are located in grassland areas.

A transient *L. curasoae* day roost is located in the study area at 1,770 m elevation. This roost is used by *L. curasoae* between late July and late September, and contained 10,000 *L. curasoae* during the study period (B. Alberti, National Park Service, pers. comm.). One other nectarivorous bat, *Choeronycteris mexicana,* also roosts in the area but occurs in colonies of a dozen or fewer individuals each (Hoffmeister, 1986). Because we worked near a *L. curasoae* roost, visitation rates by *C. mexicana* to *A. palmeri* were likely negligible.

Bat Visitation Rates—Within each of 4 concentric circles with radii of 1, 2, 3, and 4 km centered on the roost, we randomly selected flowering agaves to serve as focal plants. Over 5 nights, from sunset until sunrise, we observed foraging behavior of bats at 3 or 4 agaves within each circle for a total of 170 observation hours at 19 agaves. We observed bats from 2 through 7 August 1999, the period of peak flowering of *A. palmeri* in the region (Slauson, 2000). We sat approximately 5 m from focal plants and used night-vision scopes and tally counters to count the number of visits by feeding bats to focal plants each hour. We made no attempt to determine the number of repeat visits individuals might have made to plants.

We measured 8 factors at each focal plant: inflorescence height, total number of umbels, number of umbels containing blooming flowers, relative vertical position along the inflorescence of umbels containing blooming flowers, density of flowering *A. palmeri* within a 200-m radius of the focal plant, distance and orientation from the bat roost, and elevation. We quantified forage resources available at each plant by counting the total number of umbels and number of umbels containing blooming flowers per plant. Flowering occurs sequentially from the bottom to the top of the plant, so that at any point in time, 1 to 7 umbels could contain blooming flowers. During our study, no focal agaves had blooming flowers in the upper umbels of inflorescences. All focal plants were located either east or west of the bat roost because elevation exceeded what is tolerable to *A. palmeri* north of the roost, and we did not have access to areas to the south (Mexico).

To determine which characteristics explained bat visitation rates, we analyzed variation in the number of visits per plant per hour (square-root transformed) using stepwise multiple regression. Because explanatory variables describing focal plants were correlated, we also used a principal components analysis to ordinate explanatory variables, then regressed number of visits per plant per night (square-root transformed) against the first 3 components to determine if these combinations of factors provided additional insight to this plant-animal interaction.

RESULTS—Visitation rates of bats to agaves varied considerably both among plants at any given time and within plants at different times. Visitation rates per plant ranged from 0 to 1,023 visits per hr, and averaged 273 (SE = 17, n = 170). The widest range of visitation rates to 1 plant during 1 night was from 21 to 1,023 visits per hr.

Five of the 8 characteristics that we measured explained variation in bat visitation rates (Table 1). Visitation rates were strongly associated with time of night and showed a sharp decline between midnight and sunrise (Fig. 1A). Visitation rates were associated with 2 spatial factors: visitation rates decreased as distance from the roost increased and were higher at plants east of the roost than at plants west of the roost (Fig. 1B). Visitation rates also were associated with 2 structural characteristics of plants: visitation rates increased as the number of flowering umbels per plant increased (Fig. 1C) and increased as the relative position of the flowering umbels progressed from the bot-

TABLE 1—Factors that explained variation ($P < 0.05$, from stepwise multiple regression) in visitation rates of *Leptonycteris curasoae* to *Agave palmeri,* southeastern Arizona, 1999.

Factor	Estimate	*SE*	*P*-value
Time of night (hours after sunset)	−0.79	0.17	<0.0001
Orientation from roost (east or west)	−11.3	1.47	<0.0001
Distance from roost (km)	−0.002	0.01	0.0004
Number of flowering umbels	1.02	0.37	0.0073
Relative vertical position of flowering umbels	7.25	3.25	0.0272

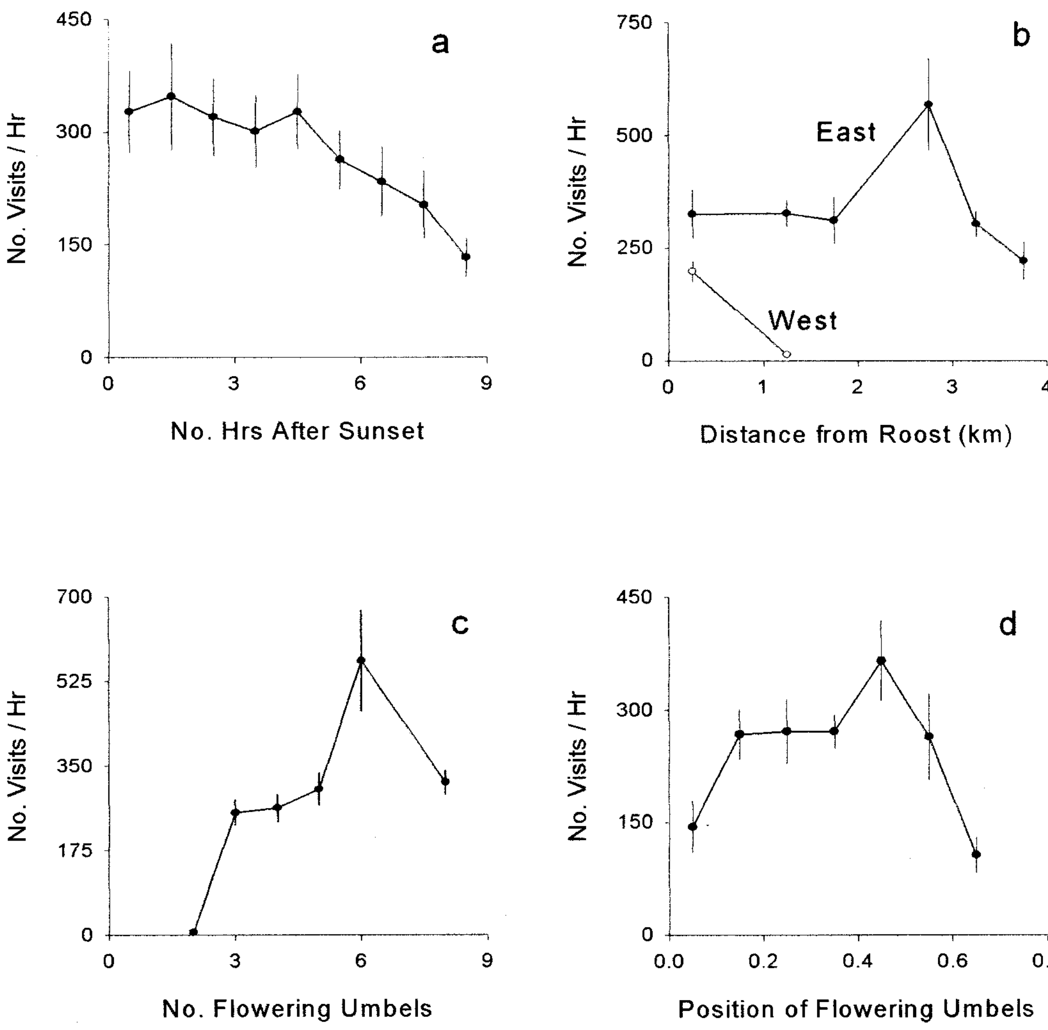

FIG. 1—Relationships among visitation rates of *Leptonycteris curasoae* to *Agave palmeri* in southeastern Arizona, 1999, versus a) time of night, b) distance and orientation from roost (closed and open circles represent plants east and west of roost, respectively), c) number of flowering umbels, and d) relative vertical position of flowering umbels along inflorescences (0.5 represents flowering umbels located centrally). Vertical bars denote ±1 *SE.*

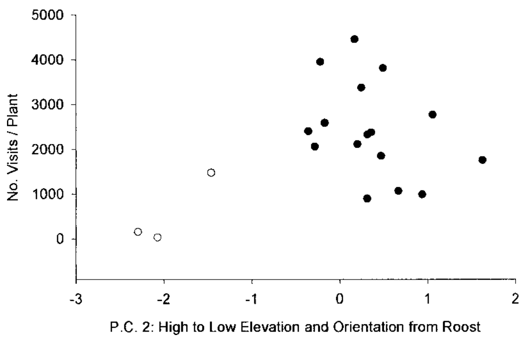

Fig. 2—Relationship between visitation rates of *Leptonycteris curasoae* to *Agave palmeri* versus the second principal component of 8 explanatory variables (PC 2), showing separation of plants east of the roost (solid circles) from those west of the roost (open circles) in southeastern Arizona, 1999.

tom toward the middle of the inflorescence and then decreased thereafter (Fig. 1D). Inflorescence height, total number of umbels per plant, density of nearby flowering conspecifics, and elevation did not explain appreciable variation in bat visitation rates ($P > 0.14$).

Three characteristics of focal plants were correlated: total number of umbels with number of flowering umbels ($r = 0.67$), number of flowering umbels with plant height ($r = 0.72$), and plant height with total number of umbels ($r = 0.85$). The first principal component (PC 1) principally reflected these 3 plant characteristics and explained 41% of total variation in bat visits per night. The second principal component (PC 2) reflected elevation and orientation from the roost and explained 21% of total variation in bat visits per night, and the third principal component (PC 3) reflected density of nearby flowering agaves and explained 11% of total variation in bat visits per night. Only PC 2 explained significant variation in bat visitation rates ($P = 0.02$; $P > 0.34$ for PC 1 and PC 3) (Fig. 2).

Discussion—Temporal variation in visitation rates of *L. curasoae* to *A. palmeri* within a night paralleled nectar production by agaves (Fig. 1A). *A. palmeri* produce nectar between 2000 and 0600 h, with peak production between 2100 and 2400 h and a gradual decrease until dawn (Slauson, 2000). Similar trends in nectar production are characteristic of plants pollinated by *L. curasoae* in other parts of their range, such as several species of columnar cacti in northwestern Mexico (Fleming et al., 1996) and Venezuela (Nassar et al., 1997). In all of these plant species, highest nectar production coincides with the time bats emerge from day roosts and energy demands are greatest.

The decrease in visitation rates by bats to agaves farther from the roost might be explained by 2 factors. First, plants farther from the roost require bats to expend more energy for travel, so visiting nearer plants is more energy efficient. Second, as bats disperse from the roost in all directions, the amount of area encountered increases with increasing distance, so the likelihood of bats encountering a flowering plant decreases. Plants closest to roosts, therefore, should be visited more often than plants farther from roosts.

Leptonycteris curasoae from this region commuted to foraging areas up to 28 km from the roost where they spent the majority of the night before returning (Ober, 2000). In this study, however, we observed *L. curasoae* present within 4 km of the roost throughout the entire night (Fig. 1A). Individuals using distant foraging areas might need to visit plants relatively close to the roost shortly after emergence to gain energy before beginning the commute, thus contributing to high visitation rates at plants close to the roost during the first few hours after sunset, while other individuals forage at plants near the roost throughout the night.

Visitation rates differed between plants located east and west of the roost (Table 1, Fig. 2). *A. palmeri* grows much more densely in grasslands, which dominated areas east of the roost, than in oak woodland (Gentry, 1982), which dominated areas west of the roost. Although density of conspecifics within a 200-m radius of focal plants did not explain variation in bat visitation rates, foraging *L. curasoae* select areas of relatively high agave density on a landscape scale (Ober, 2000). The low number of bat visits to plants west of the roost relative to those east of the roost likely reflected the relatively low density of *A. palmeri* found in the oak-woodland plant community.

Visitation rates increased with the number of umbels containing blooming flowers. Plant species that rely on animals to transport pollen attract potential pollinators with visual or aromatic stimuli (Faegri and Van der Pijl, 1966).

Hummingbirds and insects visit large plants or large inflorescences more frequently than small plants or small inflorescences (Pyke, 1981; Geber, 1985; Cruzan et al., 1988). Bats likely selected agaves with the largest visual or aromatic stimuli (i.e., those with the greatest number of umbels with blooming flowers) because these were producing the greatest amount of nectar and therefore offered the greatest energy rewards.

Visitation rates also increased as the relative vertical position of umbels containing blooming flowers progressed from the bottom to the middle of the inflorescence, and then decreased again as the vertical position of flowering umbels rose toward the top. This pattern might reflect response of the bats to resource abundance at a small scale. Umbels in the middle of *A. palmeri* inflorescences tend to contain more flowers than those located farther up or down the flowering stalk (Slauson, 1995) and therefore provide the most nectar. Other studies indicate that pollinators visit plants with many flowers more often than plants with few (Heinrich, 1975; Augspurger, 1980; Real and Rathcke, 1991). Therefore, *L. curasoae* might have been attracted to umbels with larger floral displays.

Two plant characteristics correlated with the number of umbels containing blooming flowers—total number of umbels and inflorescence height—did not explain any additional variation in visitation rates. This suggests that bats did not rely strongly on either echolocation or vision to locate plants, because these characteristics related to inflorescence size did not affect visitation rates. The number of flowering umbels did influence visitation rates ($P = 0.007$), suggesting olfaction as a possible mechanism by which bats locate flowering agaves. Observations of *L. curasoae* visiting other agave species also have suggested this (Arizaga et al., 2000).

Two factors that related to flowering stage explained visitation rates—number of umbels containing blooming flowers and the relative vertical position of those umbels. These factors relate directly to the number of nectar-producing flowers per plant and provide cues as to the amount of nectar available to pollinators from a given plant during a given night. Both of these factors change throughout the flowering season, and, therefore, bat preferences likely shift among plants accordingly.

A. palmeri flowers only once during its 10 to 30 year lifetime and dies shortly thereafter (Schaffer and Schaffer, 1979). The number of plants within *A. palmeri* populations that flower each year varies considerably, as is the case with other desert perennials, such as *Agave deserti* (Nobel, 1992) and *Yucca elata* (Laslei and Ludwig, 1985). The number of flowering *A. palmeri* in our study area was low during our study compared to the previous year (mean = 0.8 ± 0.4 plants/ha in 1999 vs. mean = 3.5 ± 0.4 plants/ha in 1998; Ober, 2000), so bats might have been less selective during this study than in years when more flowering plants were available. Furthermore, visitation rates probably were relatively high at all agaves observed, partly because all focal plants were located within 4 km of a roost containing 10,000 bats. We recommend that future research cover a larger geographic region to assess whether the patterns we found hold true in areas with fewer foraging bats, and for a longer time period to determine whether these patterns occur throughout the course of the entire flowering season.

Dietary specialization of *L. curasoae* on a single plant makes these bats vulnerable during the months they inhabit southeastern Arizona. Recovery of *L. curasoae* in this region will depend on the continued existence of *A. palmeri* populations. We found that bat visitation rates to individual forage plants were influenced by both the location of plants relative to the bat roost, as well as the flowering stage of plants. Because flowering stage is a factor that changes over the course of a single season, the importance of individual plants will shift during this time frame. This, coupled with the sparse, patchy distribution of *A. palmeri* across the landscape, suggests that conservation and recovery of *L. curasoae* will depend upon the cooperation of a large number of landowners and resource managers across the region.

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Literature Cited

Arends, A., F. J. Bonaccorso, and M. Genoud. 1995. Basal rates of metabolism of nectarivorous bats (Phyllostomidae) from a semiarid thorn forest in Venezuela. Journal of Mammalogy 76: 947–956.

Arizaga, S., E. Ezcurra, E. Peters, F. Ramirez de Arellano, and E. Vega. 2000. Pollination ecology of *Agave macroacantha* (Agavaceae) in a Mexican tropical desert. II. The role of pollinators. American Journal of Botany 87:1011–1017.

Augspurger, C. K. 1980. Mass-flowering of a tropical shrub (*Hybanthus prunifolius*): influence on pollinator attraction and movement. Evolution 34: 475–488.

Berger, M., and J. S. Hart. 1974. Physiology and energetics of flight. In: Farner, D., and J. R. Kings, editors. Avian biology, volume 4. Academic Press, New York. Pp. 416–477.

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

Cockrum, E. L. 1991. Seasonal distribution of northwestern populations of the long-nosed bats, *Leptonycteris sanborni* family Phyllostomidae. Anales del Instituto de Biologia Universidad Nacional Autonoma de Mexico, Serie Zoologica 62:181–202.

Cruzan, M. B., P. R. Neal, and M. F. Willson. 1988. Floral display in *Phyla incisa*: consequences for male and female reproductive success. Evolution 42:505–515.

Dafni, A. 1992. Pollination ecology: a practical approach. IRL Press, Oxford, United Kingdom.

Faegri, K., and L. van der Pijl. 1966. The principles of pollination ecology. Pergamon Press, New York.

Fleming, T. H., M. D. Tuttle, and M. A. Horner. 1996. Pollination biology and the relative importance of nocturnal and diurnal pollinators in three species of Sonoran Desert columnar cacti. Southwestern Naturalist 41:257–269.

Geber, M. A. 1985. The relationship of plant size to self-pollination in *Mertensia ciliata*. Ecology 66: 762–772.

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

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.

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.

Hoffmeister, D. F. 1986. Mammals of Arizona. University of Arizona Press, Tucson.

Howell, D. J. 1972. Physiological adaptations in the syndrome of chiropterophily with emphasis on the bat *Leptonycteris* Lydekker. Unpublished Ph.D. dissertation, University of Arizona, Tucson.

Laslei, R. J. G., and J. A. Ludwig. 1985. Fruit production by *Yucca elata* Engelm. (Liliaceae) in four Chihuahuan Desert habitats. Southwestern Naturalist 30:321–322.

Nassar, J. M., N. Ramirez, and O. Linares. 1997. Comparative pollination biology of Venezuelan columnar cacti and the role of nectar-feeding bats in their sexual reproduction. American Journal of Botany 84:918–927.

Neuweiler, G. 2000. The biology of bats. Oxford University Press, New York.

Nobel, P. S. 1992. Annual variations in flowering percentage, seedling establishment, and ramet production for a desert perennial. International Journal of Plant Science 153:102–107.

Ober, H. K. 2000. Foraging ecology of lesser long-nosed bats. Unpublished M.S. thesis, University of Arizona, Tucson.

Pyke, G. H. 1981. Optimal foraging in hummingbirds: rule of movement between inflorescences. Animal Behaviour 29:889–896.

Real, L. A., and B. J. Rathcke. 1991. Individual variation in nectar production and its effect on fitness in *Kalmia latifolia*. Ecology 72:149–155.

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.

Sellers, W. D., R. H. Hill, and M. R. Sanders. 1985. Arizona climate: the first hundred years. University of Arizona Press, Tucson.

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. 1995. Factors affecting the distribution, pollination ecology, and evolution of *Agave chrysantha* Peebles and *A. palmeri* Engelm. (Agavaceae). In: Biodiversity and management of the Madrean Archipelago. United States Department of Agriculture, Forest Service, General Technical Report RM-GTR-264. Pp. 194–205.

Slauson, L. 2000. Pollination biology of two chiropterophilous agaves in Arizona. American Journal of Botany 87:825–836.

Thomas, S. P. 1975. Metabolism during flight in two species of bats, *Phyllostomus hastatus* and *Pteropus gouldii*. Journal of Experimental Biology 63:273–

293.
UNITED STATES FISH AND WILDLIFE SERVICE. 1995. Lesser long-nosed bat recovery plan. United States Fish and Wildlife Service, Albuquerque, New Mexico.
VON HELVERSEN, O., AND H. U. REYER. 1984. Nectar intake and energy expenditure in a flower visiting bat. Oecologica 63:178–184.

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