ACTIVITY PATTERNS AND ROOST SELECTION BY *NOCTILIO ALBIVENTRIS* (CHIROPTERA: NOCTILIONIDAE) IN COSTA RICA

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Using radiotracking and direct observation we documented activity patterns and roost selection of *Noctilio albiventris* at the Estación Experimental Enrique Jiménez Nuñez near Cañas, Costa Rica. Bats with radiotransmitters showed little consistency in their use of foraging areas. Observations of captive and free-flying animals suggested that time away from the roosts represented foraging time. Individual bats showed considerable variation in both foraging time and numbers of foraging bouts per night, but total time away from the roost usually averaged 120 min/night. Bats with radiotransmitters roosted in hollow trees and, although most used the same roosts repeatedly, some changed roosts during the study period.

Key words: *Noctilio albiventris*, radiotracking, activity, roosting, Costa Rica

Radiotracking of bats has provided information about foraging activity and roosting behavior not necessarily available from other methods of study. Animal-eating bats show three distinct patterns of activity (Fenton, in press). Some species hunt from continuous flight and fly for virtually the whole night (e.g., *Euderma maculatum*—Wai-Ping and Fenton, 1988; *Nyctalus noctula*—Kronwitter, 1988; *Myotis myotis*—Audet, 1990; *Lasiurus cinereus*—Barclay, 1989). Other continuous fliers spend only ca. 2 h on the wing (e.g., *Scotophilus borbonicus*—Fenton and Rautenbach, 1986; *Lasiurus borealis*—Hickey and Fenton, 1990; *Eptesicus fuscus*—Brigham, 1991). Still other species fly for much shorter periods, hunting alternately from continuous flight, and from perches (e.g., *Nycteris grandis*—Fenton et al., 1990; *Megaderma lyra*—Audet et al., 1991). Because of the high cost of flight, these three foraging strategies have different energetic consequences whether prey are taken in flight (e.g., *E. maculatum, E. fuscus, N. noctula, L. borealis, L. cinereus, S. borbonicus*), or from surfaces (e.g., *M. myotis, M. lyra, N. grandis*).

Sometimes data from radiotracking of individual bats have confirmed impressions from captures in mist nets or observations of populations of foraging bats. For example, mist netting indicates that some species have peak activity at dusk, and scattered activity through the night (e.g., *E. fuscus, S. borbonicus*). In other cases, data from individuals with radiotransmitters reveal patterns of activity that differ substantially from those suggested by captures or observation (e.g., *L. borealis, E. maculatum*). *L. borealis* with radiotransmitters, e.g., are only active for ca. 2 h/night, even though population studies suggest continuous activity (Hickey

and Fenton, 1990; Kunz, 1973). Similarly, captures of *E. maculatum* indicated a peak in activity at mignight (Watkins, 1977), while observation of individuals and monitoring general foraging indicate activity throughout the night (Wai-Ping and Fenton, 1988).

Radiotracking also has revealed two patterns of roost fidelity among bats. Some return night after night, year after year to the same roost, while others occupy a different roost almost every night (Fenton and Rautenbach, 1986). In species such as *E. fuscus,* the pattern of roost occupancy varies geographically, and by roost structure (Brigham, 1991). Roosts are key resources for many bats, providing shelter, protection from predators, and an opportunity to reduce metabolic costs (Bell et al., 1986; Kunz, 1982; Roverud and Chappell, 1991).

Noctilio albiventris is a 30–35-g bat of the Neotropics and captures in mist nets suggest a bimodal pattern of nightly activity (Brown, 1968; Hooper and Brown, 1968). These bats roost in tree hollows, or in buildings (Hood and Pitocchelli, 1983) and use high-intensity echolocation calls to locate and track their prey (Brown et al., 1983; Roverud, 1987). While the larger *Noctilio* (*N. leporinus*) eats fish and often feeds heavily on invertebrates (Brooke, 1991), *N. albiventris* appears to depend more on insects than on fish (Howell and Birch, 1974). Still, *N. albiventris* forages over water, and its attack behavior resembles that of the larger *Noctilio* (Suthers and Fattu, 1973). *N. albiventris* realizes considerable energetic savings by roosting with conspecifics (Roverud and Chappell, 1991), making roost selection, and association with a group, important.

The purpose of this study was to use radiotracking to examine the flight activity pattern of *N. albiventris,* which is thought to have a bimodal pattern of flight activity based on captures in mist nets (Brown, 1968; Hooper and Brown, 1968). We also documented roost selection and patterns of habitat use by this bat at the Estación Experimental Enrique Jimenez Nuñez (10°20′N,

85°08′W; Fig. 1), near Cañas, Guanacaste Province, Costa Rica.

MATERIALS AND METHODS

On 3 and 4 January 1992, we captured 17 *N. albiventris* in mist nets (star in circle; Fig. 1) and used Skin Bond® surgical adhesive to attach 0.9-g radiotransmitters (Holohil Systems Ltd., Woodlawn, Ontario, Canada, K0A 3M0) to eight bats, two females caught on 3 January, and two males and four females caught on 4 January. All females were nonreproductive and all males nonscrotal. The bats taken on the second night were caught within 20 min of one another, in mist nets, set ca. 50 m from one another. One radiotransmitter, attached to a male, malfunctioned after 2 nights. The bats receiving radiotransmitters had body masses ranging from 28.7 to 32.6 ($\pm$0.1, $n = 8$) g (Ohaus, Portogram balance), making the transmitters 3.1–2.7% of the bats' body masses, well under the 5% mass threshold for which radiotransmitter load may affect the bat's flight performances (Aldridge and Brigham, 1988). All bats were released within 60 min at the capture sites.

Between 5 and 16 January we monitored the bats' activity using two Merlin-12 receivers (Custom Electronics, Urbana, IL 61801) equipped with five-element collapsible Yagi antennae and a Lotek SRX 400 Telemetry (scanning) Receiver (Lotek Microelectronic Design and Manufacture, Aurora, Ontario, Canada, L4G 3J9) using either a Yagi or an omnidirectional antenna. The scanning receiver always was located at the roost tree (B of Fig. 1), recording the presence or absence of bats with radiotransmitters every 10 min. From 1745 h, pairs of observers, in contact by radio, monitored the movements of bats with radiotransmitters. This approach, combined with the scanning station, permitted all-night monitoring of the bats' behavior until the morning of 16 January.

We used two hand-held, battery operated, halogen spotlights to observe bats foraging over the aquaculture ponds, where we listened for the echolocation calls of *Noctilio* with narrowband bat detectors tuned to 60 kHz (Ultra Sound Advice Mini-2 or Batbox-2 detectors). Results are expressed as $\bar{X} \pm SD$.

RESULTS

On the morning of 5 January, we located seven of the *N. albiventris* with radiotrans-

mitters roosting in a ca. 30-m tall *Aldizia coribacaea* tree (B in Fig. 1), which had one large opening at the base, and other openings in large branches scattered throughout the canopy, referred to hereafter as the main roost. Although the bats used other tree roosts, on 51 of at least 55 bat-days (one bat-day = a bat with an active transmitter for 24 h), they spent the day in the main roost. On 5 January, one female occupied an unidentified hollow tree (A in Fig. 1) close to the main roost. In the daylight hours of 8 and 9 January, another female roosted in a 30-m tall hollow *Terminalia catarpo* tree (C in Fig. 1), ca. 500 m from the main tree. This bat shared this roost, on both days, with one *Desmodus rotundus* that had a radiotransmitter (J. Long, pers. comm.), and other bats that did not have radiotransmitters. Another female emerged from the main roost at dusk on 8 January, and did not return by dawn on 9 January. The bat visited the main roost for 10 min at 1850 h on 11 January, but we could not locate her alternate day roost.

On 4 evenings, solitary observers watched the emergence of bats from near the base of the main roost tree, starting at 1740 h. Although 200–500 bats emerged from openings near the base of the canopy, few used the lower opening. Three sizes of bats roosted in the tree. The largest (*N. albiventris*) and the smallest species used high-intensity echolocation calls, conspicuous at 20–30 m to bat detectors tuned from 30–80 kHz.

Noctilio albiventris with radiotransmitters typically emerged from the roost tree just as it began to get dark, ca. 30 min after sunset. The average of 51 recorded departures was 1758 h ± 6 min, and actual times ranged from 1748 h to 1823 h local time. These data, for known individuals, are similar to those obtained for the population of bats roosting in the tree, as observed from below.

Using radiotracking data, we documented the time spent away from the roost for seven bats (one male, six females) on a total of 40 bat-nights. To be included in this data
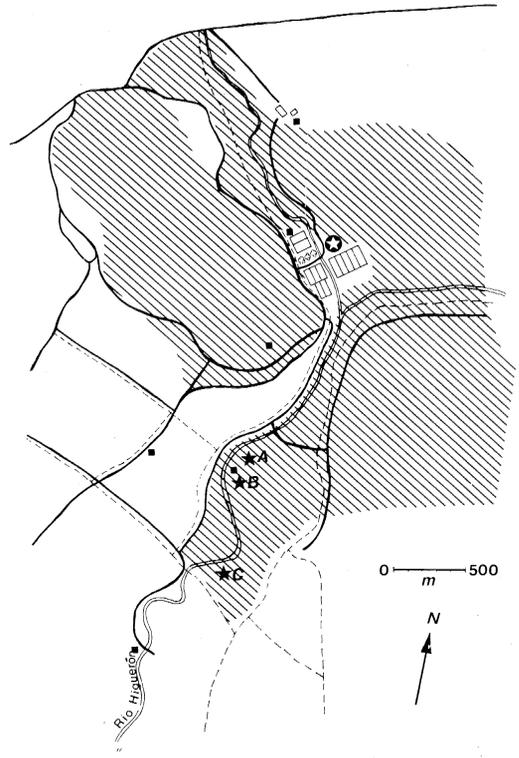

FIG. 1.—A map of the study area showing the locations of roosts and information about captures of *Noctilio albiventris* near Cañas, Costa Rica. Roads are indicated by solid lines, the Rio Cañas by a channel. The dashed lines show the positions of irrigation canals. The hatched lines indicate forested areas, and the open areas are cleared fields or pastures. The open star in a black circle denotes the places where the bats were captured, the solid stars the three roost trees referred to in the text. Solid squares identify radiotracking stations. The rectangles show the locations of the aqualculture ponds.

set, the bat with a radiotransmitter had to have been in the main roost tree before dark, and after dawn, on any given night. Bats with radiotransmitters made one (*n* = 14) or several flights a night (15 two flights, 8 three flights, and 3 four flights). The basic patterns are illustrated as cumulative flight times for the night of 8–9 January (Fig. 2). Although the pattern of single versus multiple flights varied among individuals, there were no significant trends (χ^2 = 17.72, *d.f.*
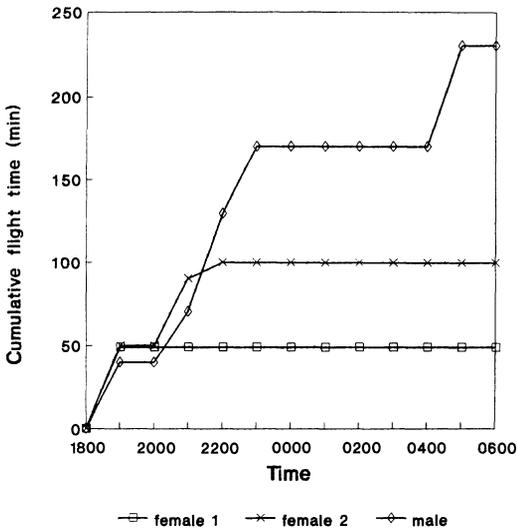
Fig. 2.—Cumulative flight times of *Noctilio albiventris* on the night of 8–9 January 1992 for three individuals, illustrating different patterns of behavior.

= 18; $P = 0.50$). During the 10 nights of the study, each of the seven bats with radiotransmitters made only one flight on at least 1 night.

Total time away from the roost averaged 117.6 ± 81.2 min/night ($n = 40$), and an ANOVA indicated that bats making more than one flight a night were away significantly ($F = 14.81$; $P = 0.0004$; $d.f. = 38$) longer ($\bar{X} = 148 \pm 84.2$ min) than those that made one flight ($\bar{X} = 59.7 \pm 24.5$ min). Bats that made one flight on any given night were absent from the roost for longer than the first periods of absence when two ($\bar{X} = 41.3 \pm 18.1$; $n = 15$), three ($\bar{X} = 42.5 \pm 25.8$ min; $n = 8$), or four ($\bar{X} = 41.7 \pm 16.1$ min; $n = 3$) flights were involved. The durations of additional absences varied from $\bar{X} = 90.4 \pm 46.9$ min ($n = 15$) for two absences, to $\bar{X} = 51.3 \pm 42.7$ min ($n = 8$) for three, and $\bar{X} = 76.7 \pm 115.5$ min ($n = 3$) for four. The differences in lengths of first absences are not significant among bats and nights ($F = 2.0$; $P = 0.2$; $d.f. = 21$) showing no evidence of an inherent pattern.

The *N. albiventris* we caught and equipped with radiotransmitters were taken within 50 m of the aquaculture ponds (Fig. 1). Furthermore, the 15 bats caught on 4 January all were taken in a period of ca. 20 min. From 1800 h on 4 January, there was a steady stream of *N. albiventris* flying north. In spite of these initial observations, *N. albiventris* with radiotransmitters rarely foraged over the aquaculture ponds. Specifically, three bats used the ponds on 5 of the 10 nights we radiotracked from there. On 6 January, one female arrived at the ponds at 1814 h, and spent 30 of 61 min away from the main roost flying over, and around, the ponds. On 7 January, this bat arrived at the ponds at 1803 h, remained there until 1807 h when she flew out of range, returning at 1847 h. The bat spent 21 min flying over the ponds before returning to the main roost. We never detected signals from the bats with radiotransmitters around the ponds during later flights away from the roosts.

Each night that we sampled with spotlights at the ponds ($n = 6$ nights), we observed *N. albiventris* foraging there. In the 1st hour after dark, up to 75 *N. albiventris* flew back and forth over the ponds, usually within 0.5 m of the water surface. Monitoring with bat detectors, and observations with spot lights, revealed a peak in numbers of foraging *N. albiventris* over the ponds for ca. 30 min, beginning just after dark (1800 h). Their flight behavior, and the incidence of feeding buzzes (high pulse-repetition rates coinciding with attacks on airborne prey—Griffin et al., 1960), indicated that these bats were foraging. Bats rarely were seen at that site after 1900 h.

DISCUSSION

Our data for individuals demonstrate that although some show a bimodal pattern of flight activity as suggested by captures in mist nets (Brown, 1968; Hooper and Brown, 1968), others make one flight a night and still others three or four flights. Furthermore, individuals vary the numbers of flights they make from night to night. Our data, therefore, do not support the generalization

from population studies about the flight activity of *N. albiventris*. Away from roosts, bats with radiotransmitters flew continuously in habitats ranging from fields and pastures to ponds and woodlands. Over the ponds, these flights coincided with feeding by *N. albiventris* without radiotransmitters, so we propose that flight time away from roosts coincided with periods of foraging. Bimodality in flight periods in this species, and others such as *E. fuscus* (Brigham, 1991), *S. borbonicus* (Barclay, 1985; Fenton and Rautenbach, 1986) or *L. borealis* (Hickey and Fenton, 1990), appears to support this interpretation. If we are correct, *N. albiventris* forages for ca. 120 min each night, unlike other species that fly for much longer, or much shorter, periods (see above). Variation in foraging time could reflect choice of food, or even digestive efficiency (Barclay et al., 1991), and in other species is significantly affected by reproductive condition (Brigham, 1991).

Our radiotracking and observation data from *N. albiventris* showed that these bats did not return repeatedly to the same foraging site, either at different times during the night, or from night to night. In this, the bats resemble *E. fuscus*, from eastern Canada (Brigham, 1991), or *S. borbonicus*, from Zimbabwe or South Africa (Barclay, 1985; Fenton and Rautenbach, 1986). The *Noctilio* we studied were less consistent in their use of foraging areas than *E. maculatum* (Wai-Ping and Fenton, 1988), and much less so than either *L. borealis* (Hickey and Fenton, 1990), or *L. cinereus* (M. B. C. Hickey, pers. comm.), where individuals return to the same specific foraging sites night after night (both species), and year after year (*L. cinereus*).

The data also provide further information about patterns of roost fidelity in nonbreeding bats. Although some of the bats we equipped with radiotransmitters visited and used at least four day roosts (three in hollow trees), they changed day roosts less often than *S. borbonicus* (Fenton, 1983; Fenton and Rautenbach, 1986), or *E. fuscus*

(Brigham, 1991), that also roost in hollow trees. In their roost occupancy, the *N. albiventris* resembled *D. rotundus,* which also roosts in hollow trees (Wilkinson, 1985). Tree size is one obvious difference in the roosts used by these four species. The main roost of *N. albiventris* in our study was large (diameter at breast height >1.5 m), while the tree roosts of *S. borbonicus* and *E. fuscus* were <1 m in diameter at breast height (Brigham, 1991; Fenton and Rautenbach, 1986). *Rhinolophus hildebrandti* showed roost fidelity similar to *N. albiventris,* when the day roost was a large (>2 m in diameter at breast height) baobab tree (Fenton and Rautenbach, 1986).

Tree size nothwithstanding, there is no obvious pattern to the roost-fidelity strategies of different bats. Roost structure, such as tree size, trees versus buildings, or different kinds of crevices, is known to affect the consistency of roost occupancy (e.g., Brigham, 1991; Fenton et al., 1985; Fenton and Rautenbach, 1986; S. Lewis, pers. comm.). Roost structure can limit occupancy time, the best example coming from *Thyroptera tricolor* roosting in furled *Heliconia* leaves (Findley and Wilson, 1974). Other available roosts, however, are used only from time to time, including hollows (citations above) and tents (Timm and Mortimer, 1976). Patterns of roost consistency also vary in species that roost in foliage, with changes in general (Fenton et al., 1985) or specific (Morrison, 1980) roost location.

Although the risk of predation often is invoked to explain roost-switching behavior in bats (Fenton, 1983; Kunz, 1982), sometimes bats continue to use a roost in spite of direct attacks (e.g., *R. hildebrandti*—Fenton and Rautenbach, 1986), while in other species, the disturbance of attack leads to a temporary abandonment of a roost (*M. myotis*—Audet, 1990). Although we caught a predatory bat (*Vampyrum spectrum*) within 50 m of the main roost tree, we saw no evidence of predation on the *N. albiventris* we studied. Roost switching in tent-making bats also has been

related to predation (Timm and Clawson, 1990).

Parasite loads may affect patterns of roost occupancy (also see Wilkinson, 1985), and at least four of the *N. albiventris* we captured were heavily infested with mites. Furthermore, the patterns of pupal emergence of some bat ectoparasites seem adaptive to survival over periods when roosts are not occupied. For example, Marshall (1971) observed that the pupal stage of a nycteribiid fly could last up to 50 days, presumably giving the flies the ability to survive periods when no food was available. Our data provide no support for the hypothesis that roost-switching reflects the incidence of ectoparasites.

Literature Cited

ALDRIDGE, H. D. J. N., AND R. M. BRIGHAM. 1988. Load carrying and maneuverability in an insectivorous bat—a test of the 5% "rule" of radio-telemetry. Journal of Mammalogy, 69:379–382.

AUDET, D. 1990. Foraging behavior and habitat use by a gleaning bat, *Myotis myotis*. Journal of Mammology, 71:420–427.

AUDET, D., D. KRULL, G. MARIMUTHU, S. SUMITHRAN, AND J. B. SINGH. 1991. Foraging behavior of the Indian false vampire bat, *Megaderma lyra* (Chiroptera: Megadermatidae). Biotropica, 23:63–67.

BARCLAY, R. M. R. 1985. Foraging strategies of the tropical bat *Scotophilus leucogaster*. Biotropica, 17: 65–70.

———. 1989. The effect of reproductive condition on the foraging behavior of female hoary bats, *Lasiurus cinereus*. Behavioral Ecology and Sociobiology, 24:31–37.

BARCLAY, R. M. R., M. A. DOLAN, AND A. DYCK. 1991. The digestive efficiency of insectivorous bats. Canadian Journal of Zoology, 69:1853–1856.

BELL, G. P., G. A. BARTHOLOMEW, AND K. A. NAGY. 1986. The roles of energetics, water economy, for-

aging behavior and geothermal refugia in the distribution of the bat, *Macrotus californicus*. Journal of Comparative Physiology, 156:441–450.

BRIGHAM, R. M. 1991. Flexibility in foraging and roosting behaviour by the big brown bat (*Eptesicus fuscus*). Canadian Journal of Zoology, 69:117–121.

BROOKE, A. 1991. The diet of *Noctilio leporinus*. Bat Research News, 33:67.

BROWN, J. H. 1968. Activity patterns of some Neotropical bats. Journal of Mammalogy, 49:754–757.

BROWN, P. E., T. W. BROWN, AND A. D. GRINNELL. 1983. Echolocation, development and vocal communication in the lesser bulldog bat, *Noctilio albiventris*. Behavioral Ecology and Sociobiology, 13: 287–298.

FENTON, M. B. 1983. Roosts used by the African bat *Scotophilus leucogaster* (Chiroptera: Vespertilionidae). Biotropica, 15:129–132.

———. In press. Volant insectivores. *In* Insect-eating mammals: evolution and adaptations for insectivory (C. R. Dickman, ed.). Cambridge University Press, Cambridge, United Kingdom.

FENTON, M. B., AND I. L. RAUTENBACH. 1986. A comparison of the roosting and foraging behaviour of three species of African insectivorous bats (Rhinolophidae, Vespertilionidae and Molossidae). Canadian Journal of Zoology, 64:2860–2867.

FENTON, M. B., R. M. BRIGHAM, A. M. MILLS, AND I. L. RAUTENBACH. 1985. The roosting and foraging areas of *Epomophorus wahlbergi* (Pteropodidae) and *Scotophilus viridis* (Vespertilionidae) in Kruger National Park, South Africa. Journal of Mammology, 66:461–468.

FENTON, M. B., C. M. SWANEPOEL, R. M. BRIGHAM, J. E. CEBEK, AND M. B. C. HICKEY. 1990. Foraging behavior and prey selection by large slit-faced bats (*Nycteris grandis*; Chiroptera: Nycteridae). Biotropica, 22:2–8.

FINDLEY, J. S., AND D. E. WILSON. 1974. Observations on the Neotropical disk-winged bat, *Thyroptera tricolor*. Journal of Mammalogy, 55:562–571.

GRIFFIN, D. R., F. A. WEBSTER, AND C. R. MICHAEL. 1960. The echolocation of flying insects by bats. Animal Behaviour, 8:141–154.

HICKEY, M. B. C., AND M. B. FENTON. 1990. Foraging by red bats (*Lasiurus borealis*): do intraspecific chases mean territoriality? Canadian Journal of Zoology, 68:2477–2482.

HOOD, C. S., AND J. PITOCCHELLI. 1983. Noctilio albiventris. Mammalian Species, 197:1–5.

HOOPER, E. T., AND J. H. BROWN. 1968. Foraging and breeding in two sympatric species of Neotropical bats, genus *Noctilio*. Journal of Mammalogy, 49:310–312.

HOWELL, D. J., AND D. BURCH. 1974. Food habits of some Costa Rican bats. Review Biologica Tropica, 21:281–294.

KRONWITTER, F. 1988. Population structure, habitat use and activity patterns of the noctule bat, *Nyctalus noctula* Schreb. 1774 (Chiroptera: Vespertilionidae) revealed by radio-tracking. Myotis, 26:23–85.

KUNZ, T. H. 1973. Resource utilization: temporal and spatial components of bat activity in central Iowa. Journal of Mammalogy, 54:14–32.

———. 1982. Roosting ecology. Pp. 1–56, *in* Ecology

of bats (T. H. Kunz, ed.). Plenum Press, New York, 425 pp.

MARSHALL, A. M. 1971. The ecology of *Basilia hispida* (Diptera: Nycteribiidae) in Malaysia. The Journal of Animal Ecology, 40:141–154.

MORRISON, D. W. 1980. Foraging and day-roosting dynamics of canopy fruit bats in Panama. Journal of Mammalogy, 61:20–29.

ROVERUD, R. C. 1987. The processing of echolocation sound elements in bats: a behavioural approach. Pp. 152–170, *in* Recent advances in the study of bats (M. B. Fenton, P. A. Racey, and J. M. V. Rayner, eds.). Cambridge University Press, Cambridge, United Kingdom, 470 pp.

ROVERUD, R. C., AND M. A. CHAPPELL. 1991. Energetic and thermoregulatory aspects of clustering behavior in the Neotropical bat *Noctilio albiventris*. Physiological Zoology, 64:1527–1541.

SUTHERS, R. A., AND A. FATTU. 1973. Fishing behaviour and acoustic orientation by the bat (*Noctilio labialis*). Animal Behaviour, 21:61–66.

TIMM, R. M., AND B. L. CLAWSON. 1990. A roof over their feet. Natural History, 90:55–58.

TIMM, R. M., AND J. MORTIMER. 1976. Selection of roost sites by Honduran white bats, *Ectophylla alba* (Chiroptera: Phyllostomatidae). Ecology, 57:385–389.

WAI-PING, V., AND M. B. FENTON. 1988. Ecology of spotted bat (*Euderma maculatum*): roosting and foraging behavior. Journal of Mammalogy, 70:617–622.

WATKINS, L. C. 1977. Euderma maculatum. Mammalian Species, 77:1–4.

WILKINSON, G. S. 1985. The social organization of the common vampire bat. I. Pattern and cause of association. Behavioral Ecology and Sociobiology, 17:111–122.