

MORPHOLOGICAL CHARACTERISTICS PREDICT ALTERNATE FORAGING STRATEGY AND MICROHABITAT SELECTION IN THE ORANGE-BELLIED BAT, *LAMPRONYCTERIS BRACHYOTIS*

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Neotropical bat species may coexist because they forage in different places or in different ways. The small insectivorous orange-bellied bat, *Lampronycteris brachyotis* (Phyllostomidae), differs from coexisting gleaners in key ecomorphological characteristics, including longer, narrower wings and smaller ears. Using telemetry, we measured range size, range use, and activity patterns, and assessed habitat preferences for 9 individuals for 50 nights over 4 months on Barro Colorado Island, Panama. The bats spent the night in individual, medium-sized (22–27 ha) foraging areas within forested regions close to shorelines, up to 4 km away from the day roost. Each bat spent most of its time in a small (3–5 ha) core area. Foraging flights ranged from a few s to more than 70 min. Total flight time per night averaged 3.5 h and flight distance was estimated to be 60 km. There were no distinct activity peaks. Our tracking data suggest that *L. brachyotis* primarily forages in the canopy, where it gleans insects from vegetation in a combination of perch hunting and continuous flight. This species may also catch insects in air above the canopy. This unique behavior among gleaning insectivorous phyllostomids corroborates our hypothesis that morphological adaptations combined with behavioral flexibility reflect distinct differences in foraging strategies and microhabitat selection. We conclude that differential use of space and hunting strategies promotes coexistence among the species-rich guild of Neotropical insectivorous gleaning bats.

Key words: Barro Colorado Island, bat community, coexistence, *Lampronycteris brachyotis*, Neotropics, Panama, Phyllostomidae, spatial use, telemetry

Among mammals, the species-rich order of bats (Chiroptera) successfully uses an exceptionally wide range of habitats and resources at night (Arita and Fenton 1997). As in most vertebrates, species richness increases dramatically from temperate zones toward the tropics, where more than 100 species may coexist in local communities (Findley 1993; Lim and Engstrom 2001; Simmons and Voss 1998). Tropical bats are often the most abundant mammals in local species assemblages and play crucial roles as pollinators, seed dispersers, and insectivores. However, our understanding of factors that lead to and maintain high diversity of bats in local communities is still limited.

Following the original guild concept developed for birds (Root 1967), bats can be sorted into functional groups, or guilds, according to their diet, foraging habitat, and foraging strategy (e.g., Bonaccorso 1979; Findley 1993; Kalko et al.

1996; Schnitzler and Kalko 1998). Although temperate-zone bats are exclusively insectivorous, (sub)tropical bats reveal a wide dietary spectrum. This dietary diversity is particularly well represented in the family of leaf-nosed bats (Phyllostomidae), encompassing insects, small vertebrates, and blood as well as pollen, nectar, fruit, and leaves (Findley 1993; Gardner 1977). Phyllostomids forage in a wide array of habitats ranging from obstacle-rich space in the forest interior to less cluttered space near forest edges and in forest gaps. It is, however, still unclear to which degree they might also use the open space away from clutter, such as areas above the canopy. Bats also employ a range of foraging strategies. They capture insects on the wing (aerial) or collect food from surfaces (gleaning), the latter either in short flights from perches or in continuous flight (Fenton 1990; Schnitzler and Kalko 1998).

Community studies on tropical birds convincingly show that within guilds, microhabitat selection, and in particular, vertical stratification, resource use, foraging strategies, and trophic diversity, contribute substantially to high levels of diversity (Terborgh et al. 1990). For tropical bats, a few inventories suggest that vertical stratification may also play an important role (Bernard 2001; Bonaccorso 1979; Kalko and Handley

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TABLE 1.—Mass and measures of size of 85 adult *Lampronycteris brachyotis* on Barro Colorado Island, Panama.

Characteristic	Males		Females	
	$\bar{X} \pm SE$	<i>n</i>	$\bar{X} \pm SE$	<i>n</i>
Mass (g)	12.6 ± 0.3	40	12.5 ± 0.3	38
Forearm (mm)	39.1 ± 0.2	38	40.4 ± 0.3	35
Tibia (mm)	17.5 ± 0.1	38	18.2 ± 0.1	35
Testis length (mm)	4.3 ± 0.3	19	—	—
Testis width (mm)	3.0 ± 0.2	16	—	—
No. of ectoparasites	1.5 ± 0.3	28	1.9 ± 0.4	20

2001), but no detailed species-specific behavioral data are available to test this pattern. Our limitation in knowledge of bats stems mainly from difficulties applying methods for studying highly mobile nocturnal animals. As a result, community studies on bats have relied heavily on ecomorphological approaches (e.g., Findley 1993; Fleming 1986; Swartz et al. 2003; Willig 1986). However, morphological characteristics of bats alone do not necessarily reveal the whole range of ecological niche differentiation (Saunders and Barclay 1992), given the high degree of behavioral flexibility exhibited by bats (Fenton 1990). Among the many species of phyllostomids, most behavioral field studies have focused on fruit-eating bats (e.g., Charles-Dominique 1986; Fleming 1993; Handley et al. 1991), with only few observations on gleaning insectivorous-carnivorous species (Humphrey et al. 1983; Kalko et al. 1999).

We studied the small orange-bellied bat, *Lampronycteris brachyotis* (Phyllostomidae), which occurs from Mexico to the Amazon basin, and evaluated how well morphological characteristics may predict the bat's behavior, and how microhabitat selection and foraging strategies may facilitate coexistence within the species-rich guild of insectivorous gleaners. *L. brachyotis* is considered a rare species, although it regularly occurs in inventories within its range (Kalko et al. 1996; Simmons and Voss 1998). Its diet consists mainly of insects that are allegedly gleaned in the understory of tropical forests, although fruit has occasionally been reported in the diet (Medellín et al. 1985). Compared with other, coexisting insectivorous gleaners, *L. brachyotis* has distinctly smaller ears in proportion to its body size (Reid 1997: plate 8). This is an unusual feature for gleaners because they typically have large ears that support detection of food using prey-generated sounds such as rustling noises or advertisement calls (Fenton 1995; Schnitzler and Kalko 1998). Furthermore, its wings are longer and narrower than those of sympatric gleaners.

Because of its distinct morphology, we hypothesized that *L. brachyotis* would forage in more open habitat and spend more time on the wing than sympatric gleaners. We propose that niche partitioning based on differences in microhabitat selection, activity pattern, and foraging strategy are driving forces in promoting coexistence among Neotropical bats.

MATERIALS AND METHODS

Study site.—We conducted our 4-month field study (1 February to 31 May 2000) in Panama on Barro Colorado Island (BCI; 9°9'N, 79°51'W; area 15.6 km²; elevation 27–171 m) and on the adjacent

Buena Vista peninsula. BCI and Buena Vista are separated by a 400-m-wide channel. The area is covered with seasonal lowland semideciduous forest consisting of a mosaic of older (400–600 years) and younger patches (70–100 years). The climate is characterized by a distinct dry season from mid-December through April, with 10% of the total annual rain (2,600 mm), and a wet season with a monthly precipitation of 300 mm. Mean day and night temperatures are 27°C and 25°C, respectively (forest, 20 m aboveground; Windsor 1990).

Study species.—After several revisions, *Lampronycteris* (Chiroptera: Phyllostomidae, Phyllostominae) is now treated as a monotypic genus (Wetterer et al. 2000). *L. brachyotis* is distributed from southern Mexico to the Brazilian Amazon basin including Trinidad. It occurs from sea level up to 525 m (Medellín et al. 1985 and references therein). For our study, all tracked bats were captured on BCI at a day roost in a hollow trunk of a *Dipteryx panamensis* (Fabaceae) tree in old secondary growth (about 100 years). The exit hole was at ground level and the conical cavity inside the tree was about 5 m high with a basal area of 0.7 × 1 m. At least 200 bats roosted in the tree, including mostly *L. brachyotis*, but also some *Trinycteris nicefori*, and a few *Carollia perspicillata* (Phyllostomidae).

To estimate range size and use, we radiotracked 9 individuals (5 adult nonreproductive females and 4 adult males) chosen from a total of 85 captured individuals (39 females, 46 males). For each individual we documented sex, age, condition of teeth (pointy, worn) and wing membranes (no, few, many scars), reproductive status, mass (to nearest 0.5 g; 100-g spring balance, Pesola, Baar, Switzerland), length of forearm and tibia (to nearest 0.5 mm; metal ruler), and number and type of ectoparasites (Diptera: Streblidae; Acari; Table 1). Our data on morphology, reproductive condition, and parasite load are concordant with literature data (Medellín et al. 1985).

Telemetry.—We used small transmitters (BD2-AP, Hohloh Systems, Carp, Ontario, Canada; mass 1.038 g ± 0.02 SD), which represent 6.9–9.4% of the mass of the bats. Using a hand-held antenna (5-element Yagi, Wildlife Materials, Carbondale, Illinois) and a Yaesu receiver (FT-290R II, Wagener Telemetrieanlagen, Cologne, Germany), the range of transmitters within the forest was up to 300 m in contrast to open space, where signals could be detected up to 2.5 km. After fur was clipped, radiotransmitters were glued onto bats' backs with surgical glue (Histoacryl, Braun Surgical, Melsungen, Germany). Tagged bats (females [designated F₁–F₅] and males [designated M₁–M₄]) were released at their day roost within 2 h after capture. We collected data beginning the night after capture for 1 individual at a time as long as the transmitter lasted (4–7 days). Two observers were in continuous radio contact (Yaesu FT-26, Wagener Telemetrieanlagen) with each other during tracking. To assess spatial size and use, we triangulated each bat's position by taking simultaneous bearings at 3-min intervals. Intervals were shortened only when bats rapidly changed their position. Bearings were taken from trails within the forest and from boats attached to fixed positions in the lake (stumps, buoys), and located with a global positioning system (TSC1, precision 1 m, Trimble, Sunnyvale, California). Positions of tracked bats were located acoustically by assessing each signal's intensity (bearing error, 7–12°). To ensure accuracy, we avoided small (0–15°) and large (165–180°) bearing angles between the 2 observers. Transmitters were equipped with a mercury position switch that provided information on the bats' activity through changes in the repetition rate of the signal at a precision of 1 s. We defined the activity phase to be the time between the 1st emergence of *L. brachyotis* from the day roost in the evening until the last entry in the morning.

Bearings were analyzed using the computer program Tracker (Camponotus 1994). A geographic map was imported into the program to visualize locations of each bat. Of 9 tagged bats, 5

(M₁, M₃, M₄, F₄, and M₅) were tracked in the wet season and 4 (F₁–F₃ and M₂) were tracked in the dry season. Triangulation data were collected on 50 nights. Time of contact, where at least 1 of the 2 observers received an unambiguous signal, was very high (98% or 499 of 514 tracking h). Of a total of 3,037 data points, 2,701 (89%) were selected for final analysis. We discarded 11% as noncrossing bearings or clearly erroneous, extreme outliers.

Analysis of range size and use.—To overcome inherent limitations on range size and use of telemetry data, we chose 2 methods. We calculated home range size with the minimum convex polygon method (MCP), where the outermost bearings are connected to form a mononuclear area. We estimated range use (foraging and core areas) with the probabilistic kernel method (adaptive Gauss; density coefficient of variation of 0.15; Worton 1989). Often, telemetry data are temporally autocorrelated (Harris et al. 1990), especially in areas associated with concentrated resources (food, roosts, partners). It is an intrinsic characteristic of data for spatial use and movement patterns of animals that they are nonrandom and temporally dependent (de Solla et al. 1999). For data collection we followed White and Garrot (1990), who recommended choosing a time interval long enough to allow an animal to potentially cross its home range (in this study, 3 min). Hence, possible autocorrelation of our data was determined by the animals' behavior. Finally, MCP and kernel are nonparametric analyses and thus both applicable to autocorrelated data (Cresswell and Smith 1992).

Home range.—We defined home range following Burt (1943:351) as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young." However, to avoid overestimation of home ranges, we excluded day roosts and commutes between day roosts and foraging areas of 7 bats (F₁–F₅ and M₁, M₂) that used night roosts differently from day roosts. In all individuals cumulative home range size approached a plateau during the respective tracking period. For each bat we therefore pooled data for home range size.

Foraging and core areas.—Foraging areas encompassed an area that is used by a bat for gathering and processing food. Core areas are defined as preferred regions within a home range (Samuel et al. 1985). To avoid overestimation of night roost sites where bats partially spent substantial time, we calculated both areas including only tracking data for flying bats. To determine size of a foraging area, we chose the isopleth containing 95% of the points (White and Garrot 1990) and calculated core areas with 50% isopleths.

Activity rhythm and foraging modes.—To assess activity rhythm of *L. brachyotis*, we divided nights into eleven 1-h intervals (1900 to 0600 h) and measured cumulative mean flight time for each interval. We evaluated differences in flight time per interval (s/h) between sexes and within h over the night (2-way repeated measures analysis of variance [ANOVA]; normally distributed data universe: chi-square test, $P = 0.37$, $n = 502$). To describe foraging modes, we divided flight durations of 9 *L. brachyotis* into 4 classes: very short flights (1–10 s), short flights (11–60 s), long flights (>1–20 min), and very long flights (>20 min).

RESULTS

Range size.—Eight of 9 tracked *L. brachyotis* had their entire home range on BCI. The home range of 1 female (F₄) was located on nearby Buena Vista peninsula. All home ranges were located close to the shoreline (Fig. 1). Four females (F₁–F₃, F₅) used old forest in the southern part of BCI, whereas home ranges of 1 female (F₄; Buena Vista) and of all 4 males (northwestern part of BCI) were located in areas of younger forest. Median home range size was not statistically different (Mann–Whitney U -test: $z = -0.12$, $P = 0.9$) between 4 males



FIG. 1.—Home ranges (minimum convex polygon) of 9 *Lamproncycteris brachyotis* on Barro Colorado Island and Buena Vista, Panama. Grid: 1 km.

(33 ha) and 5 females (32 ha), although mean home ranges were twice as large in males (61 ha) as in females (34 ha) because 1 male (M₂) used 2 foraging areas (Fig. 1; Table 2). However, exclusion of M₂ from the calculation leads to a similar mean home range size in males (28 ha) as that in females.

Spatial use.—We assessed the spatial use of *L. brachyotis* by identifying foraging and core areas with the kernel method. Median size of foraging areas was slightly larger in 4 males (27 ha) than in 5 females (22 ha), without statistically significant differences (Mann–Whitney U -test: $z = -0.37$, $P = 0.7$). Median size of core areas was similar (Mann–Whitney U -test: $z = 0.09$, $P = 1.0$) in males (4 ha) and females (5 ha). For 7 individuals we identified 1 core area per foraging area, whereas 2 individuals (M₂ and F₁) used 2 core areas (Fig. 2; Table 2). Sequential tracking does not allow for conclusions about temporal overlap in spatial use. However, we found that 5 of 9 individuals (M₃, M₄ and F₁, F₂, F₅) overlapped spatially in their foraging areas. In addition, 2 of them (F₁, F₅) overlapped in the use of their core areas (Fig. 2).

Flight distance and speed.—To estimate total distance (d) flown by tracked *L. brachyotis* per night, we added direct distances between successive triangulation points (normal distribution: chi-square test, $P = 0.45$, $n = 50$). Given that this approach assumes that bats always chose a direct flight path between locations, which we know was mostly not the case, mean nightly distance ($d_{\mu} = 15.2$ km, $n = 9$, $d_{\min} = 7.6$ km, $d_{\max} = 25.2$ km; Table 2) has to be treated as a minimum value. We also calculated the product of cumulative nightly flight time (3.4 h) and flight speed. On a commuting flight between day roost and foraging area (2 km; 203 s) we assessed flight speed (9.9 m/s) for a female (F₅). Very likely, flight speed

TABLE 2.—Range and area size, number of roosts, and flight parameters of 9 *Lampronycteris brachyotis* on Barro Colorado Island, Panama. Note there were 2 core areas for M₂ and F₁.

Parameter	Males				Females				
	M ₁	M ₂	M ₃	M ₄	F ₁	F ₂	F ₃	F ₄	F ₅
Home range (ha)	46	158	20	19	48	32	26	25	41
Foraging area (ha)	40	116	11	14	57	20	22	20	42
Core area (ha)	4	7, 11	2	2	1, 6	3	5	5	10
No. of core areas	1	2	1	1	2	1	1	1	1
Distance from day roost to foraging area (km)	1.0	1.0	0	0	1.9	2.1	2.7	1.8	2.2
No. of identified night roosts	10	9	1	2	6	9	8	2	4
Mean flight distance per night (km)	16	14	9	10	14	17	17	14	16
Mean flight duration per night (h)	3.6	3.9	2.3	2.9	3.4	4.2	4.0	4.1	4.3

is slower while foraging than on commuting flights, given that similar sized bats use similar speeds (8–10 m/s) on flights in open space (Sahley et al. 1993; Winter 1999) and slower foraging flights in structure-rich understory (6 m/s; Heithaus and Fleming 1978). Hence, we took a conservative approach and used only half of the flight speed to estimate flight distance (Winter 1999). This resulted in a relatively long flight distance that individuals flew per night ($d_{\mu} = 60.6 \text{ km} \pm 3 \text{ SE}, n = 50$).

Roosting behavior.—Fidelity to the day roost during the tracking period was high. Seven bats used the hollow *Dipteryx* tree where they were originally captured. Two individuals (M₂ and F₃) switched after the 1st night of capture to other day roosts located in areas inaccessible to us in the southern part of BCI. With the exception of 2 males (M₃, M₄), who also had the smallest foraging areas (11 and 14 ha) of all tracked *L. brachyotis*, no individual foraged near the day roost but instead flew into rather distant foraging areas (M₁ and M₂, 1.0 km; F₁–F₅, 1.8–2.7 km; Fig. 2; Table 2). Within these foraging areas all

tracked *L. brachyotis* used several night roosts (median, 6; Table 2), with the exception of 1 male (M₃), who exclusively used the day roost simultaneously as a night roost. We did not find any of the other night roosts; however, no tagged bat appeared to change night roosts during the tracking period.

Our telemetry data indicate that *L. brachyotis* frequently foraged in the upper canopy region and also used the open space above tree crowns. When we tracked the bats from a boat, we continuously received strong tracking signals over large distances (up to 2 km). This long range indicates that *L. brachyotis* was mostly flying in open, unobstructed space and not within the forest, as we tested the maximum range of small transmitters used in this study to be only about 300 m within obstacle-rich understory. In addition, we located 2 transmitters, which were still functioning after the bats had lost them, in the upper canopy, about 30 and 40 m aboveground, respectively. Finally, the use of open space was documented for 6 bats (F₁–F₅ and M₁) that frequently flew over water within their foraging areas, likely for transfer and probably also for foraging flights (Figs. 1 and 2). One of them (F₄) crossed a 400-m-wide water channel twice each night to commute between day roost and foraging area.

Nocturnal activity.—Tracked *L. brachyotis* left the day roost $45.1 \text{ min} \pm 3 \text{ SE}$ ($n = 48$) after local sunset and returned to the day roost about 1 h ($52.9 \text{ min} \pm 6, n = 45$) before local sunrise. Males flew significantly less time per h interval than females ($F = 7.0, P < 0.05$). Despite some fluctuation in activity, flight time did not differ significantly within intervals in either sex ($F = 1.32, P = 0.24$). Activity pattern of *L. brachyotis* did not follow a pronounced unimodal or bimodal pattern but was rather even (Fig. 3). Although 7 bats were continuously active during the night (mean cumulative flight time, 3.6 h), activity of the 2 males that stayed close to the day roost (M₃, M₄) was always low (Table 2). The least active bat (M₃) spent 82% of its activity phase in the day roost.

Most flights (66%; total, 1,064) lasted 1–20 min, whereas very short (11%), short (10%), and very long flights (13%) were rare, indicating that *L. brachyotis* mostly foraged during long search flights (mean, 9.5 min). Very short and short flights suggest that bats may have occasionally shifted to perch hunting with short sally or search flights. The 4 classes were evenly distributed throughout the course of the night (2-way ANOVA; 11-h intervals from 1900 to 0600 h; $F = 0.0, P = 1.0$).

Reproduction.—*Lampronycteris brachyotis* exhibited a reproductive peak during the transition between dry and wet

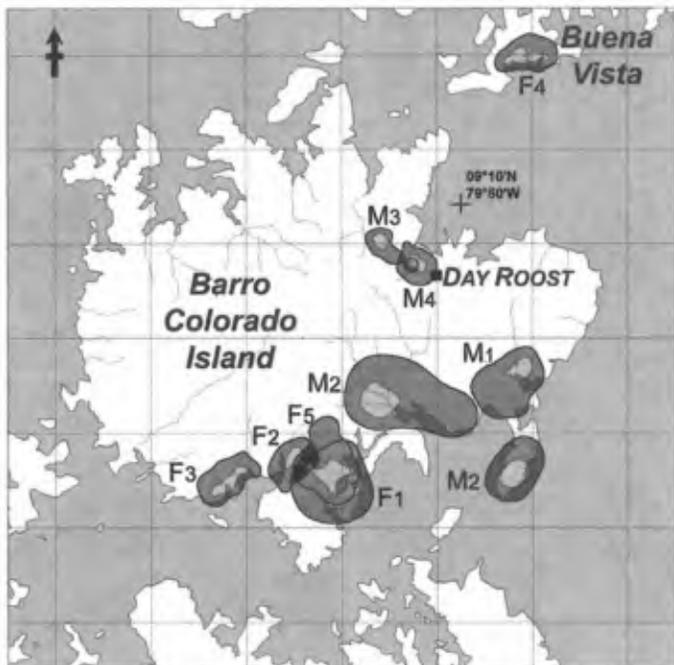


FIG. 2.—Foraging (dark; 95% kernel) and core areas (light; 50% kernel) of 9 *Lampronycteris brachyotis* on Barro Colorado Island and Buena Vista, Panama. Grid: 1 km.

season (March to May). In February, no females were palpably pregnant as opposed to March, when 75% of adult females were advanced in pregnancy. Frequency of pregnancy decreased in April (40% of females) to very low levels in May (6%). We found lactating females with young in April (33%) and May (65%). All captured lactating females ($n = 23$) had their young attached. Although most males ($n = 11$) had small testes (3–4 mm length) over the whole study period, they were larger (5–6 mm length) in 8 males that we caught in April and May, shortly after litters were produced.

DISCUSSION

In our radiotracking study on BCI, we showed that *L. brachyotis* uses relatively large home ranges to forage in extended search flights for its prey (in particular, insects) in and above the canopy. Its nocturnal flight activity is very high and does not decrease during the course of the night. This affirms our proposed hypothesis that *L. brachyotis* would forage in more open habitat and spend more time on the wing as predicted by its morphological characteristics such as relatively small ears and longer, narrower wings compared with those of sympatric gleaner species of leaf-nosed bats.

Home range size.—An important factor structuring spatial use within local communities is the size of home ranges. Unfortunately, meaningful comparisons of home range size of tropical bats are still difficult because of a lack of data collected in a standardized way. To minimize negative effects on the bat's behavior, we used the lightest motion-sensor transmitters currently available. The main disadvantage of small transmitters is their limited range, especially in tropical forests where it is reduced by high humidity and dense vegetation.

Home ranges of 9 *L. brachyotis* were relatively large (mean, 32–33 ha) compared with their small body size and mass (12 g). Compared with other species, body mass does not account for size of home range alone. Despite their large body size, 2 sympatric gleaner phyllostomids on BCI, *Lophostoma silvicolum* (31 g) and *Trachops cirrhosus* (34 g), had relatively smaller home ranges (mean, 17 and 46 ha, respectively—Bockholdt 1998; Hämsch 1998; Kalko et al. 1999) than *L. brachyotis*. In contrast, the home range of a similar sized, temperate aerial insectivorous bat, *Vespertilio murinus* (Vespertilionidae, 15 g), was twice as large (mean, 62 ha—Jaberg 1998).

Other parameters, such as wing shape, activity, and foraging strategy, may better account for home range size. Although *L. silvicolum* and *T. cirrhosus* have rather short and broad wings (low wing loading; Stockwell 2001), *L. brachyotis*, and in particular, *V. murinus*, have longer and narrower wings (high wing loading—M. Weinbeer, in litt.; Jaberg 1998), which allow faster and energetically more efficient flight (Norberg and Rayner 1987). These differences are reflected well in the nightly cumulative flight time. *L. brachyotis* flew on average more than 200 min per night, with a cumulative flight distance of about 60 km. In contrast, *T. cirrhosus* and *L. silvicolum* flew only a few km per night within less than 100 min of cumulative flight time. The flight behavior of *L. brachyotis* resembles that of aerial insectivores, which often fly long distances per night

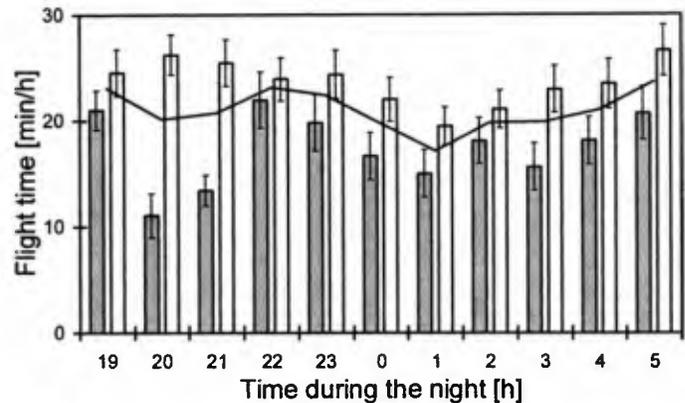


FIG. 3.—Flight time (mean \pm SE) over eleven 1-h intervals of 5 female (white) and 4 male (gray) *Lamproncyteris brachyotis* on Barro Colorado Island, Panama. Solid line: overall mean.

(Vespertilionidae, 90–100 km—Dietz 1998; K. Safi, personal communication; Molossididae, >100 km—Davis et al. 1962). We conclude that *L. brachyotis* is adapted to fly long distances (extended flights of up to 70 min) in relatively obstacle-free canopy. For foraging, it combines perch hunting behavior (short sally flights) with gleaner during extended flight (mean flight duration, 9.5 min) and probably also makes aerial captures. This is in contrast to other gleaners, in particular to *L. silvicolum* and *T. cirrhosus*, which search for food in much smaller areas exclusively in understory (Kalko and Handley 2001), where foraging is associated mainly with short flights (mean duration, <4 min—Bockholdt 1998; Hämsch 1998).

Microhabitat selection.—In contrast to other studies, where all *L. brachyotis* had been caught in forested areas away from large bodies of water (Goodwin 1969), all home ranges of *L. brachyotis* on BCI were located close to the shore of the island. Moreover, most *L. brachyotis* flew regularly in open space over the water during commuting or sometimes also foraging flights within their foraging areas. Proximity to water may be primarily caused by the small size (15.6 ha) of BCI and its extensive shore areas. However, preference of bats for shoreline habitat might also be due to increased insect abundance along the shore and above water due to hatching insects.

Commuting distance.—Home ranges of male *L. brachyotis* were closer to the day roost than were those of females. Although factors such as diet, foraging mode, spatio-temporal predictability of food, and colony size are likely to explain some individual variability (Entwistle et al. 1996; Jaberg 1998; Morrison 1980; Sahley et al. 1993), we propose that in *L. brachyotis* the mating system is the main contributing factor to this behavior. Our capture records and our data on reproductive conditions suggest that *L. brachyotis* uses a harem mating system probably coupled with a synchronized, postpartum estrus of the females, which is known for a number of species of frugivorous bats in the Phyllostomidae. Typically, dominant harem males forage in the vicinity of their day roost and frequently return to the colony (Handley et al. 1991; Morrison 1980) to ensure access to females and circumvent being usurped by other males (Kunz et al. 1998). Our observations

of 2 males (M_3 , M_4) that stayed close to the day roost throughout the tracking period are consistent with this pattern. Both males were reproductively active. In contrast, males not displaying enlarged testes and copious glandular secretions foraged further away from the day roost, as did females. A harem structure is further supported by the pattern of night roost use. We documented 2–10 different night roosts for 7 individuals, whereas the 2 presumed harem males (M_3 , M_4) used the day roost simultaneously as a night roost. One reason for the separation of day and night roost for nonharem males and females may be the location of food. It may be more efficient to stay close to feeding sites than to return to the day roost after each foraging flight (Handley and Morrison 1991).

Spatial use and foraging strategy.—Foraging areas of *L. brachyotis* make up 70–80% of home range size. In conjunction with a high number of long flights, this supports our assumption that *L. brachyotis* searches primarily for insects, which are widely distributed in space. Another important factor influencing spatial use is temporal distribution of food. *L. brachyotis* did not change foraging areas during the period of tracking. Consistency in the use of foraging areas has also been observed in bats of other guilds, such as frugivores (Fleming 1988; Thies 1998), gleaning insectivore–carnivores (Bockholdt 1998; Hämsch 1998), and aerial insectivores (e.g., Brigham 1991; Clark et al. 1993). This suggests a continuous food supply. In contrast, *Artibeus jamaicensis*, the main diet of which in many areas is figs (*Ficus*, Moraceae) that are highly abundant only for a very brief period of several consecutive nights on a tree, frequently changes its foraging area (Handley et al. 1991; Morrison 1980).

Activity.—Certain activity patterns are characteristic for individual guilds and are likely to be caused by differences in foraging strategy and food abundance. Many aerial insectivores, which prey on emerging insects at dusk and dawn, follow a bimodal activity pattern (Hayes 1997). When hunting prey that is active later at night, bats are active in a unimodal pattern (Rodríguez-Duran and Lewis 1987). In contrast, species whose food is more evenly distributed over the night, as we assume is the case for *L. brachyotis*, typically forage all night without any distinct fluctuations in activity (Fenton and Kunz 1977; Kalko et al. 1999).

Flights of *L. brachyotis* lasted from 1 s to about 70 min and were interrupted by resting periods of up to 2.5 h. Extended flights are characteristic of aerial insectivores (e.g., Dietz 1998; Jaberg 1998; Swartz et al. 2003), whereas some gleaning insectivorous–carnivorous phyllostomid bats exhibit perch hunting behavior (e.g., Hämsch 1998; Kalko et al. 1999; Wilson 1971) that is typified by hanging perched for long periods interrupted by short flights that last only a few s up to several min. We found both patterns in *L. brachyotis*, which, supported by the long and continuous high activity over more than 11 h per night, suggest a combination of 2 foraging strategies, perch hunting and gleaning from flight (Fenton 1990). This pattern in association with the assumed use of the upper canopy and aerial captures of insects in open space above the canopy supports our hypothesis that within the guild of gleaning insectivorous–carnivorous bats, fine-grained resource

partitioning through differential use of space and flexibility in foraging strategies are key factors promoting the high diversity in Neotropical bats.

We do not believe that *L. brachyotis* depends on mass emerging insects at dusk because of its late emergence from the day roost. This assumption is further supported by its even and high nocturnal activity pattern. In a preliminary analysis of fecal samples we found no fruit, which lets us suppose that *L. brachyotis* preferentially feeds on insects that are evenly distributed over the night. In addition, it might switch among several foraging strategies (Entwistle et al. 1996; Fenton 1990).

To conclude, *L. brachyotis*, 1 of at least 10 sympatric gleaning insectivorous–carnivorous phyllostomid species on BCI (Humphrey et al. 1983; Kalko et al. 1996; E. K. V. Kalko in litt.), shows a unique foraging behavior for an insectivorous Neotropical leaf-nosed bat as it appears to forage primarily in the upper canopy region and in open space along the shore of BCI. Our study affirms the link between ecomorphological characters and resource use in bats (e.g., Aguirre et al. 2002). We propose that, as in other species assemblages, fine-grained resource partitioning based on differences in size and use of foraging areas as well as differences in activity pattern and foraging strategies play key roles in structuring the species-rich Neotropical bat communities, and facilitate long-term species coexistence.

RESUMEN

Varias especies de murciélagos neotropicales pueden coexistir porque forrajean en regiones distintas o con comportamientos diferentes. El pequeño murciélago insectívoro de pecho-naranja, *Lampronycteris brachyotis* (Phyllostomidae), se distingue de otras especies de insectívoros de follaje (“gleaners”) que coexisten con él, por características ecomorfológicas clave, como alas más largas y angostas y orejas más pequeñas. Utilizando telemetría medimos tanto tamaño y uso de áreas, así como patrones de actividad y preferencias de hábitat en 9 individuos a lo largo de 50 noches durante 4 meses en la Isla de Barro Colorado, Panamá. Los murciélagos pasaron las noches en áreas de forrajeo individuales de tamaño mediano (22–27 ha) en regiones boscosas cerca de la orilla del lago Gatún hasta una distancia de 4 km desde su refugio diurno. También se determinó que cada murciélago pasó la mayoría del tiempo en pequeñas áreas centrales (3–5 ha). Vuelos de forrajeo tenían una duración de unos segundos a más que 70 minutos. El tiempo de vuelo total nocturno duraba un promedio de 3.5 horas, y la distancia de vuelo promedio fue de 60 km. No encontramos picos de actividad distintivos. Nuestros datos de telemetría sugieren que *L. brachyotis* forrajea principalmente en el dosel donde captura insectos de la vegetación, combinando la caza de percha con el vuelo continuo. Esta especie posiblemente también captura insectos en vuelo sobre el dosel. Este comportamiento único en filostómidos insectívoros de follaje apoya nuestra hipótesis que adaptaciones morfológicas combinadas con la flexibilidad de comportamiento reflejan diferencias distintivas en estrategias de forrajeo y selección de microhábitat. Concluimos que el uso diferencial de espacio y estrategias de caza promueven coexistencia en el

grupo diverso de especies de murciélagos neotropicales insectívoros de follaje.

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