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HOME-RANGE SIZE AND SPACING PATTERNS OF *MACROPHYLLUM MACROPHYLLUM* (PHYLLOSTOMIDAE) FORAGING OVER WATER

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We studied home-range size and patterns of range use of long-legged bats, *Macrophyllum macrophyllum* (Phyllostomidae), at Barro Colorado Nature Monument, Panama, by using radiotelemetry. Movements of 4 males and 5 females fitted with radiotransmitters were monitored for 4–7 entire nights each between April and July 2002. *M. macrophyllum* had an extensive range compared to other similar-sized phyllostomid bats. Median home-range size for the 9 individuals tracked was 23.9 ha (range 7.3–150.7 ha). With a median of 17.3 ha (range = 7.3–24.9 ha), home ranges of males were somewhat, but not significantly, smaller than those of females (44.4 ha, range = 16.3–150.7 ha). The bats foraged exclusively over water, whereby hunting activity was restricted to the immediate shoreline of Gatun Lake. Foraging areas ranged from 2.7 to 96.1 ha, with a median of 12.3 ha for both sexes. In general, there was high night-to-night consistency in the use of foraging areas. Most bats had multiple foraging and core areas. Core-use areas corresponded to approximately 35% of the bats' foraging areas and were larger in females (median = 5.3 ha, range = 1.1–54.1 ha) than in males (3.3 ha, range = 2.6–8.7 ha). Maximum range span varied from 0.5 to 7.5 km, whereby males in general and 1 tracked harem male in particular foraged much closer to the day roost than did females. Individual *M. macrophyllum* traveled an estimated 35–47 km on a nightly basis, and females moved significantly greater distances than did males. Our results do not provide support for the proposition that small bats typically have small home ranges. In contrast, we conclude that foraging strategy, diet, dispersion of food resources, and wing morphology are generally better predictors of home-range size. Furthermore, reproductive condition, as well as intraspecific competition linked to colony size or social status, also strongly affect the spacing behavior and movement patterns of these bats. Our results suggest that, although *M. macrophyllum* employs a gleaning foraging strategy, it closely parallels aerial insectivorous bats in terms of range size and movement distances.

Key words: Barro Colorado Nature Monument, Chiroptera, *Macrophyllum macrophyllum*, movement patterns, radiotracking, Panama

Bat assemblages in the tropics are characterized by extraordinarily high species diversity; in Amazonian lowland forests, for instance, communities may be composed of more than 100 sympatric species that occur in geographically small areas (Kalko 1998; Voss and Emmons 1996). Hence, a central issue in community ecology is to get a better understanding of how these species-rich assemblages are organized and how the many morphologically or ecologically similar species coexist. For many taxa, including tropical bats, it has been demonstrated that differential use of space can be an important factor structuring local communities (Findley 1993; Kalko et al. 1996). Yet current knowledge about size of home ranges, range use, and partitioning of space between co-occurring species of tropical bats is still scant. The few results available point to differential use of space among feeding guilds and suggest that temporal and spatial segregation of feeding areas and foraging activity may separate species within guilds (Kalko 1998). Distinct differences in space use appear to be tightly linked to size of the animals and their foraging strategy as well as to availability and distribution of resources (Fleming 1988; Handley et al. 1991; Kalko et al. 1999; Morrison 1978).

Fostered by recent advances in transmitter miniaturization, radiotracking has proven a particularly powerful technique for

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investigating many aspects of bat ecology, including home-range requirements and patterns of space and habitat use. However, so far most detailed radiotracking studies have concentrated on temperate-zone species (e.g., Catto et al. 1996; Entwistle et al. 1996; Leonard and Fenton 1983; Robinson and Stebbings 1997; Wai-Ping and Fenton 1989), whereas relatively few studies have been conducted in the tropics (e.g., Bernard and Fenton 2003; Charles-Dominique 1991; Fenton et al. 1993; Fleming 1988; Gannon and Willig 1997; Kalko et al. 1999; Morrison 1978; reviewed in Kalko 1998).

With about 150 species, New World leaf-nosed bats (Phyllostomidae) are dominant components of local bat faunas in neotropical lowland forests. Phyllostomid bats are ecologically highly diverse and unparalleled in their feeding habits, exploiting a wide selection of foods, ranging from fruit, leaves, nectar, and pollen to insects and other arthropods, small vertebrates, and blood (e.g., Findley 1993; Kalko et al. 1996). Although radiotracking studies have long focused on frugivorous members of this speciose family (Charles-Dominique 1991; Fleming 1988; Handley et al. 1991; Heithaus et al. 1975; Morrison 1978; Thies 1998), insectivorous species have just started to receive some attention (Bernard and Fenton 2003; Kalko et al. 1999; Weinbeer and Kalko 2004).

In the present study, we investigated home-range size and patterns of range use of a small insectivorous phyllostomid bat species, the long-legged bat (*Macrophyllum macrophyllum* (Schinz, 1821)), at a lowland tropical moist forest site in central Panama. *M. macrophyllum*, the sole species of the genus, occurs from southern Mexico to Peru, northern Argentina, and southeastern Brazil (Harrison 1975). Apart from some anecdotal reports in the literature on sporadic mist-net captures and brief descriptions of day roosts (Dickerman et al. 1981; Harrison and Pendleton 1974; Seymour and Dickerman 1982), information on ecology and behavior of the species is very limited. *M. macrophyllum* is a small, slender bat, with adults having a mass of 6–9 g (Harrison 1975). In addition to the prominent, lanceolate noseleaf, which is reflected in the species' scientific name, the peculiar anatomy of the posterior extremities, including a broad interfemoral membrane (uropatagium), long legs, and large feet with powerful claws (Harrison 1975), makes *M. macrophyllum* readily distinguishable from all other phyllostomid bats. Previous field observations by several authors (Gardner 1977; Harrison and Pendleton 1974) and our own findings (Weinbeer et al., in press) indicate that *M. macrophyllum* forages primarily over water, where it gleans insects either directly from the water surface or captures airborne prey close above water. Despite their high dietary diversity, most phyllostomid bats typically forage close to or within obstacle-rich forests, where they glean food from vegetation or the ground (Kalko 1998). Hunting over water as seen in *M. macrophyllum* thus constitutes a unique foraging behavior in an atypical habitat within the Phyllostomidae, making this species particularly interesting for study.

The specific objectives of our study were to assess space use of *M. macrophyllum*, including individual variability and gender-specific differences in home-range size and patterns of range and habitat use; to evaluate whether this species conforms to the general trend that smaller bats should travel shorter distances and have smaller home ranges than larger ones (cf. Fenton 1997); and to increase our knowledge about the importance of partitioning of space in promoting the high diversity of phyllostomid bats.

MATERIALS AND METHODS

Study site.—The study was conducted from April to July 2002 at Barro Colorado Nature Monument (9°10′N, 79°51′W), Republic of Panama. Barro Colorado Island, the largest of the about 200 islands in Gatun Lake, forms the heart of this 5,600-ha biological reserve. The vegetation is classified as tropical moist forest (Holdridge et al. 1971). The climate is highly seasonal. Barro Colorado Island receives an average of approximately 2,600 mm of rainfall per year, with a pronounced dry season from late December to late April or early May, during which only about 10% of the yearly precipitation occurs. In the wet season, monthly rainfall averages 300 mm, with a short, slightly drier period between August and September (Windsor 1990). Annual temperature averages 27°C, with a mean diurnal temperature range of about 9°C. Additional details on vegetation and climate can be found in Croat (1978), Windsor (1990), and Leigh (1999).

Data Collection

Capture and handling of bats.—The colony of *M. macrophyllum* studied on Barro Colorado Island was located in an old, half-sunken ship (*Barracuda*) in Laboratory Cove. At the beginning of field work in April 2002, the colony consisted of approximately 60 individuals, mostly females. Bats were captured at an opening in the ship's hull with a net consisting of 2 poles with a piece of mist net suspended loosely between them. Individuals potentially suitable for tracking were held in cloth bags and taken to the nearby laboratory. For each individual, the following information was recorded: sex, age, forearm length (measured to the nearest 0.5 mm with a caliper, Forestry Suppliers Inc., Jackson, Mississippi), and body mass (measured to the nearest 0.5 g with a 100-g spring scale, Pesola AG, Baar, Switzerland). Reproductive condition of females was assessed by palpation and visual examination as nonreproductive (nipples very small and no fetus palpable), pregnant (palpable fetus), lactating (enlarged nipples and hairless spot around nipples), and postlactating (regrowth of hair around nipples—Handley et al. 1991). In males, length and width of the testes were measured. Only adult males and adult, nonreproductive females were selected for telemetry.

The transmitters were attached to the backs of the bats below the scapulae, usually after partially trimming the fur, and tightly glued onto the skin of the bat by using histoacrylic glue (Braun Surgical, Melsungen, Germany). Recaptured individuals showed no signs of any injury that could have resulted from tagging. In an attempt to visually locate feeding bats at night, some transmitters were additionally marked with a small piece of red reflecting tape.

The bats were fitted with position-sensitive radiotransmitters broadcasting at 150 MHz (model LB-2B, Holohil Systems Ltd., Carp, Ontario, Canada). Transmitter mass was 0.84 g ± 0.02 *SD*, representing 9.5% ± 0.7% of the bats' body masses (mean body mass of the tagged individuals 9.0 g ± 0.7 *SD*). This is less than the 10% mass threshold above which transmitter mass is regarded to seriously affect an animal's foraging behavior (Brander and Cochran 1969). Based on numerous direct observations of tagged *M. macrophyllum* in the field and also considering that small bats can carry heavier loads relative to their body mass than larger species (Norberg and Rayner 1987), we conclude that transmitter mass did not negatively affect flight performance of the tagged individuals. This is also indicated by a recaptured individual that did not lose any weight during the time it had been tracked. The radiotagged animals were released at the day roost, mostly within 1.5 h after capture. Procedures used for capture and handling of bats followed guidelines established by the American Society of Mammalogists (http://www.mammalogy.org/committees/index.asp).

Radiotracking.—Starting the following night after tagging, individual bats were generally tracked for complete nights, from time of emergence until they returned to their day roost the next morning. Two observers closely followed a bat by motorboat, monitoring the bat's location by using modified YAESU VR-500 receivers (Yaesu Musen Co. Ltd., Tokyo, Japan) with handheld H-aerials (equipment adapted by Wagener Telemetrieanlagen, Cologne, Germany). We used FM radios in the field for communication and to take simultaneous bearings. Following De Solla et al. (1999), a constant time interval of 3 min was chosen between successive readings. Only during rapid movements of the bats were readings sometimes taken more frequently. Bearings to the nearest degree were taken with a compass that was attached to the antenna (accuracy of the tracking system is ±15–20 m within 100 m of the transmitter). Between foraging bouts, that is, when a bat was resting in a night roost, its position was recorded only once to avoid overrepresentation of tracking points from these locations. Bearings were taken from fixed positions by using canal buoys, custom-made buoys that were installed within a bat's home range, tree stumps, or branches to which to attach the boats. The locations of the observers at these fixed positions were georeferenced with a global positioning system (Garmin GPS12, Garmin Inc., Olathe, Kansas; accuracy 3–7 m). Together with each bearing, time, position of the 2 observers, signal pattern (fast or slow), and signal strength, along with general observations such as information about prevailing weather conditions, were recorded on a dictaphone (SONY TCM-459V, Sony, Tokyo, Japan) and later entered into Microsoft Excel spreadsheets (Microsoft Corp., Redmond, WA). A change in pulse repetition rate depending on transmitter position (higher pulse rate in horizontal position versus lower pulse rate in vertical position) allowed us to determine whether a bat was flying or roosting. A detailed account of foraging strategies and activity pattern of *M. macrophyllum* is given elsewhere (Weinbeer et al., in press).

Database.—Between April and July 2002, 10 bats (6 females and 4 males) were tagged for radiotracking. Data from 1 female that lost the transmitter by the beginning of the 3rd night of tracking were excluded from analyses. The database thus consisted of 5 females and 4 males (hereafter referred to as F1–F5 and M1–M4, respectively) that were tracked for an average of 5.3 nights ± 0.9 *SD* each. This led to 519.5 h of tracking with on average 422.5 h (82%) of contact time (range = 55–100%) during which a bat could be followed closely.

Data Analysis

Calculation of bat locations.—Radiolocations of the bats were calculated from bearings with the computer program TRACKER (version 1.1, 1994, Camponotus AB, Solna, Sweden) and plotted on a custom-made map of the study area (compiled by W. Thies, D. Kinner, D. Clark, and R. Stallard, revision 6b, 2000). Because the bats typically returned to the same foraging areas on successive nights, we pooled all bearings taken for 1 individual for analyses. TRACKER uses a maximum-likelihood method to calculate points from simultaneous bearings by triangulation. Whenever 2 observers could not take bearings simultaneously, for example, if a bat moved too quickly, its position was determined from single bearings, along which the distance of the bat from the shore was estimated based on signal strength and gain setting. Because examination of our telemetry data and numerous observations indicated that *M. macrophyllum* foraged almost exclusively in the immediate vicinity of the shoreline and did not use the forest as a hunting habitat, we considered the determination of a bat's position from single bearings in this way as reasonably accurate (cf. Bonaccorso et al. 2002; O'Donnell 2001; Winkelmann et al. 2000).

Estimation of home-range size.—As a consequence of the hunting behavior of these bats, namely to restrict their foraging activity mostly close to the shore, it was not feasible to calculate home-range size by using minimum convex polygons (Mohr 1947). This method is still the one most frequently employed in home-range studies (Harris et al. 1990), although it suffers from several severe shortcomings (Kenward et al. 2001). With the minimum convex polygon method, range size would be largely overestimated because large tracts of forest that were never visited by the bats would be incorporated in the estimate. To obtain a more realistic estimate of home-range size, we chose to delineate areas based mainly on the observed pattern of the obtained fixes and used the lakeshore as a range boundary line. Specifically, we estimated home-range size with the computer program analySIS (version 3.1, Soft Imaging System Corp., Lakewood, Colorado) as the area between the shoreline and an imaginary line at a distance of about 50 m from the shore. Choice of this value was an approximate average based on tracking data and our observations of how far the bats occasionally ventured out onto the lake. A total of 2,812 fixes (312 fixes ± 134 *SD* per bat) from 4 male and 5 female *M. macrophyllum* was used to calculate home ranges.

Analysis of range use.—For analyses of range use, point locations determined either by triangulation or from single bearings were subsequently entered into a geographical information system (ArcView 3.2, Environmental Systems Research Group, Inc., Redlands, California) and plotted on a geographical information system–based map of the study area (compiled by D. Mixon, D. Kinner, S. Wahl, and R. Stallard, version 1.1., 2002). All calculations of range use were performed by using the ArcView extension Animal Movement (Hooge and Eichenlaub 2000). The program implements the bivariate normal-density kernel as suggested by Worton (1989) and calculates a fixed-kernel utilization distribution. Following the recommendation of Seaman and Powell (1996), we used least-squares cross-validation to select the appropriate smoothing parameter.

To facilitate comparison with other studies, we used 95% kernel isopleths to delineate foraging areas (White and Garrot 1990). In contrast to the home range, foraging areas do not include the day roost and areas traversed by a bat while commuting.

Animals commonly use space in a nonuniform manner within the boundaries of their home range, typically having preferred areas where they spend most of their time (Harris et al. 1990; Samuel et al. 1985). We determined the proportion of the range that could be defined as a core area in 2 ways. First, we used the 50% contour lines of the fixed-kernel estimation to assess centers of activity, both because this allows for direct comparison of results obtained for different individuals and because it is widely employed in radiotracking studies. Second, we quantified range cores by following the procedure outlined by Wray et al. (1992). Here, an array of kernel isopleths with a decreasing percentage of included fixes (from 95% down to 20%) is produced, and the number of core areas generated for each isopleth is subsequently counted. The isopleth with the largest number of core areas is then chosen for analysis. In those cases where no additional core area was formed other than the 95% isopleth, an average of the results obtained for the other individuals (here, the 75% kernel isopleth) was used for calculations. Kernel estimations of foraging and core areas are based on 2,352 position determinations (261 ± 116 fixes per bat) because only fixes obtained at a regular time interval (3 min) were used for analysis, as recommended by De Solla et al. (1999).

We further identified number and locations of foraging and core areas of each tracked individual and calculated the distances a bat

TABLE 1.—Size of home ranges and foraging areas of 9 *Macrophyllum macrophyllum* radiotracked at Barro Colorado Nature Monument, Panama.

Individual	Home-range size (ha)	Foraging area, 95% kernel (ha)	Number of foraging areas
Males			
M1	7.31	5.70	3
M2	24.92	41.45	4
M3	10.69	9.30	2
M4	23.94	15.33	3
Median	17.32	12.32	
Interquartile range	8.16−24.68	6.6−34.92	
$\bar{X} \pm SD$			3.0 ± 0.8
Females			
F1	16.28	2.70	1
F2	21.42	28.68	1
F3	44.44[a]	12.29[a]	3
F4	78.57	4.67	1
F5	150.74[a]	96.05[a]	3
Median	44.44	12.29	
Interquartile range	18.85−114.66	3.69−62.37	
$\bar{X} \pm SD$			1.8 ± 1.1

[a] Minimum range or foraging area.

traveled on a nightly basis within its range to describe patterns of range use. Specifically, we calculated the minimum distance flown per night (based on the distance between successive fixes), as well as maximum range span, that is, the distance between the day roost and the farthest point of a bat's home range. Moreover, we quantified the distances the bats traveled when commuting from the day roost to the nearest foraging area.

Statistical analysis.—Statistical tests were performed by using STATISTICA software (version 6.0, StatSoft, Inc., Tulsa, Oklahoma). We used Mann–Whitney *U*-tests to test for differences in home-range size and patterns of range use between males and females. For all tests, $P < 0.05$ was chosen as level of significance. Because of the autocorrelated nature of the data, differences in size of foraging and core areas calculated with the kernel method were not subjected to statistical analysis. Because range sizes were generally not normally distributed, most results are reported as medians and interquartile ranges (IQRs). All other numerical results are given as mean ±1 *SD*.

RESULTS

Home-Range Size

Home-range size varied considerably among individuals (observed range 7.3–150.7 ha; Table 1; Fig. 1). Median home-range size for all individuals in this study was 23.9 ha (IQR = 13.5–61.5 ha). Although no statistically significant differences were found in home-range size based on sex ($Z = -1.35$, $P = 0.178$), females tended to have larger home ranges (44.4 ha, IQR = 18.9–114.7 ha, range = 16.3–150.7 ha) than males (17.3 ha, IQR = 8.2–24.9 ha, range = 7.3–24.9 ha). In the case of 2 females, F3 and F5, estimates of range size are minimum values because we were unable to stay in contact with the

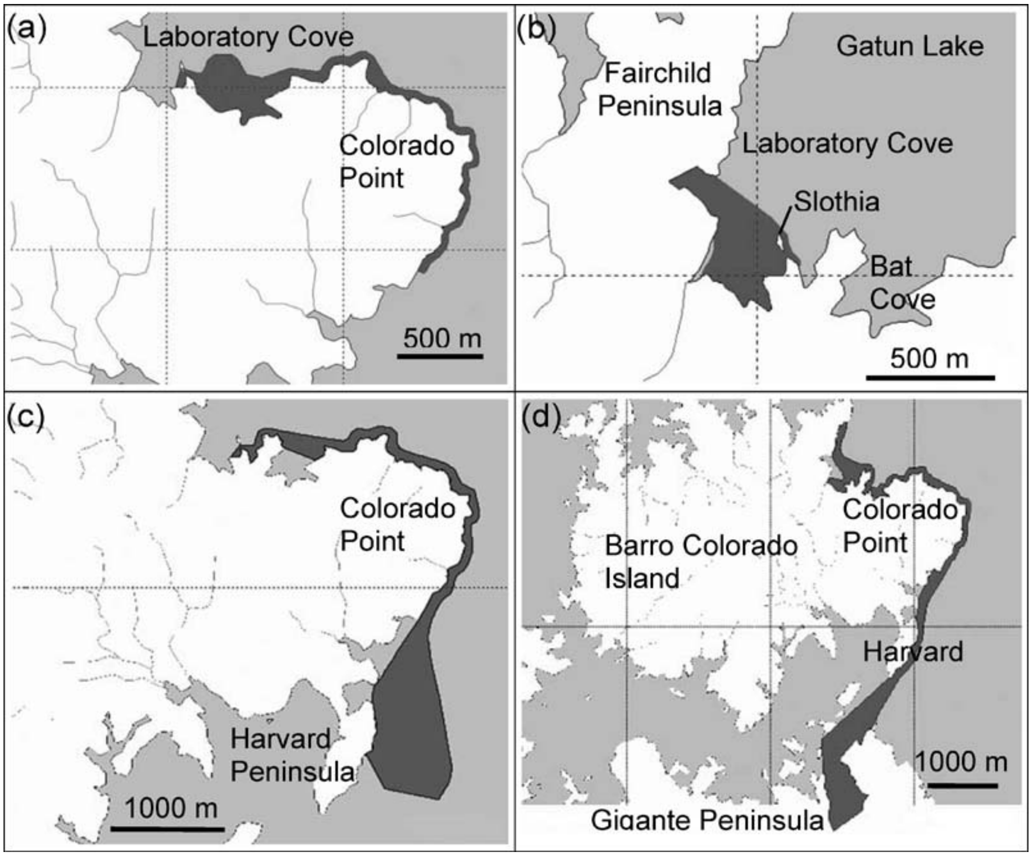

FIG. 1.—Examples of home ranges for *Macrophyllum macrophyllum* radiotracked at Barro Colorado Nature Monument, Panama, for 2 males (M) and 2 females (F). a) M2, b) M3, c) F4, and d) F5.

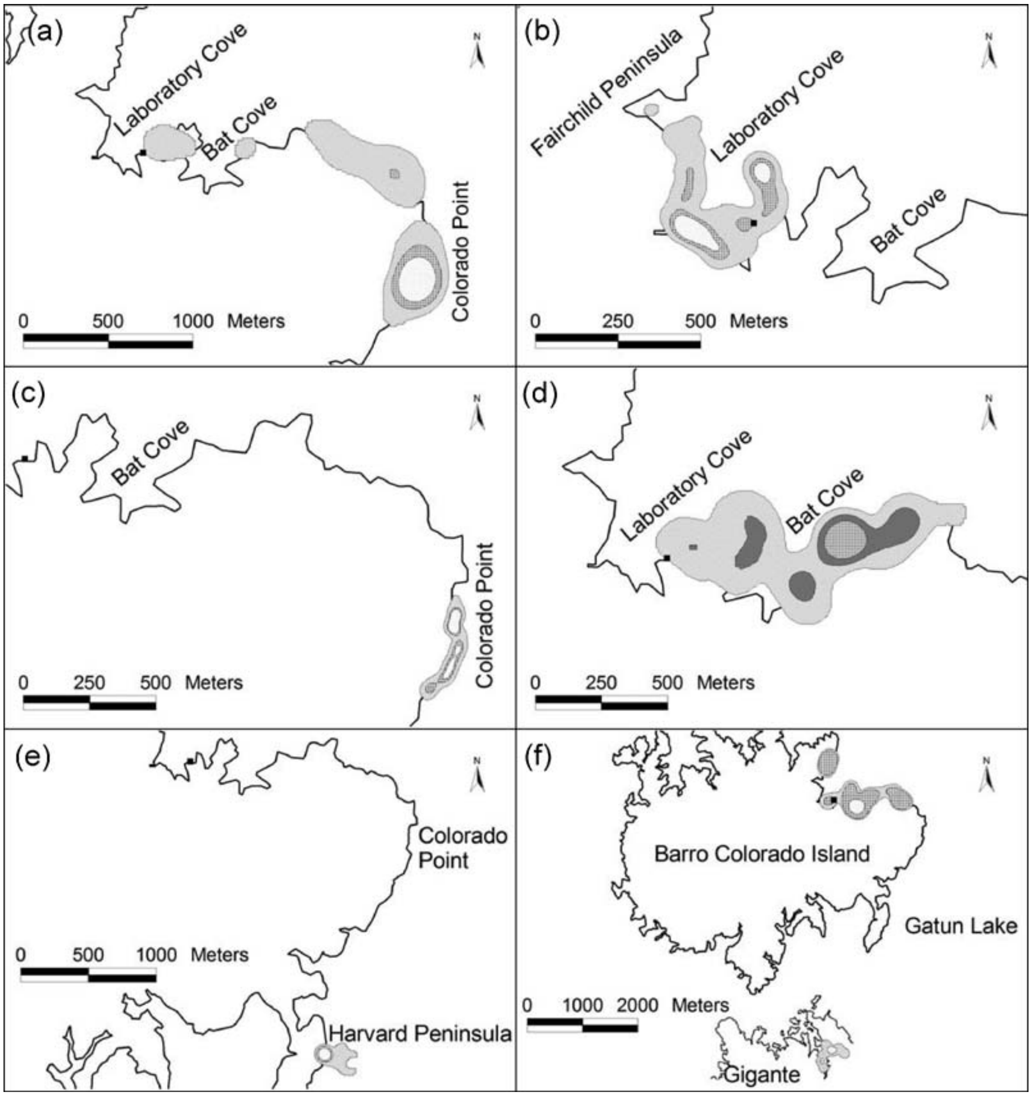

Fig. 2.—Examples of foraging and core areas for 2 male (M) and 4 female (F) *Macrophyllum macrophyllum* at Barro Colorado Nature Monument, Panama. Foraging areas, ▨; core areas as estimated by 50% kernel contour lines, ▩; core areas generated by using kernel isopleths with decreasing percentage of inclusion of fixes, ⊞. Black square, day roost in half-sunken ship, *Barracuda*. a) M2, b) M3, c) F1, d) F2, e) F4, and f) F5.

animals during their entire tracking tenure. Thus, the difference in home-range size between males and females would possibly be significant if we had been able to fully determine the home ranges of these 2 females.

Patterns of Range Use

Locations of individual home ranges, and foraging and core areas.—Examination of our tracking data indicates that *M. macrophyllum* forages exclusively over water, whereby all bats restricted their flight activity predominantly to the immediate shoreline of Gatun Lake (within approximately 50 m). This resulted in most cases in distinctly elongated home-range shapes (Fig. 1). We have no evidence that bats also used the forest as a hunting habitat. Except for bat M2, which spent most of its foraging time around Colorado Point (Fig. 2a), males in general and a harem male (M3) in particular, used small foraging and core areas that were located in Laboratory Cove or Bat Cove, that is, in close proximity to their day roost in the *Barracuda* (Fig. 2b). Females, in contrast, were much more variable, having foraging and core areas both close to and very distant from the day roost (Figs. 2c–f).

In general, moderate spatial overlap occurred between the foraging and core areas of individual bats (Fig. 2), which were distributed along the lakeshore in Bat Cove, at Fairchild and Harvard Peninsula, and around Colorado Point. During some nights 1 female (F3) crossed the Canal and spent part of the night foraging somewhere around the mainland peninsula Buena Vista. This individual thus had at least 1 other foraging area, the exact location of which could not be determined because we were not able to continuously follow this bat and obtain a sufficient number of radiofixes within that area. Bat F5 had by far the largest home range and its foraging areas were located far from one another. During some tracking nights we lost contact with the bat as it moved quickly out of the range of the receivers. On 1 night, we managed to follow this bat as it

TABLE 2.—Range use of 4 male and 5 female *Macrophyllum macrophyllum* at Barro Colorado Nature Monument, Panama. Sizes and numbers of core areas are given based on 50% contour lines of kernel estimation and as determined by the percentage inclusion of fixes that generated the isopleth with most cores.

Individual	Total core area, 50% kernel (ha)	Number of core areas, 50% kernel	Total core area, % inclusion (ha)	% of fixes in core	Number of core areas, % inclusion
Males					
M1	0.30	2	3.08	85	5
M2	4.53	1	8.72	75	2
M3	0.99	2	2.59	70	4
M4	1.15	1	3.53	75	2
Median	1.07		3.31		
Interquartile range	0.47−3.69		2.71−7.42		
$\bar{X} \pm SD$		1.5 ± 0.6		76.3 ± 6.3	3.3 ± 1.5
Females					
F1	0.58	3	1.13	65	3
F2	1.78	1	7.41	75	4
F3	2.87	1	5.26	75	1
F4	0.64	1	1.13	75	1
F5	6.02	1	54.13	90	4
Median	1.78		5.26		
Interquartile range	0.61−4.45		1.13−30.77		
$\bar{X} \pm SD$		1.4 ± 0.9		76.0 ± 8.9	2.6 ± 1.5

traveled about 7.5 km from the day roost along the Barro Colorado Island shoreline to another foraging area located around Gigante, a nearby mainland peninsula (Fig. 2f).

Foraging areas.—Median foraging areas (95% kernel) of male *M. macrophyllum* were similar in size (12.3 ha, IQR = 6.6–34.9 ha, range = 5.7–41.5 ha) but showed less variation than those used by females (12.3 ha, IQR = 3.7–62.4 ha, range = 2.7–96.1 ha). Most of the bats had several foraging areas. The number of feeding areas per individual ranged from 1 to 4 and was on average somewhat higher in males than in females (Table 1). Collectively, individuals were highly consistent in their use of foraging areas, usually returning to them night after night.

Core areas.—Main foraging activity of all tracked *M. macrophyllum* was concentrated within distinct areas of their home range. As with feeding areas, nearly all individuals used several (up to 5) core areas (Table 2). On average, core areas corresponded to only 35.2% ± 13.8% of the total size of foraging areas, but they included most of the fixes (65–90%). Median core-area size was 5.3 ha for females (IQR = 1.1–30.8 ha, range = 1.1–54.1 ha) and was somewhat smaller for males (3.5 ha, IQR = 2.7–7.4 ha, range = 2.6–8.7 ha). The large variation observed in females was mainly due to the high value for 1 individual, F5 (Table 2). These results pertain to core areas generated with kernel isopleths with decreasing percentage of inclusion of fixes. Comparative estimates of core areas based on 50% kernel isopleths are given in Table 2.

Movement patterns.—Commuting distances between day roost and nearest foraging area ranged from 0 to 4.35 km, with no significant difference between the sexes (males: median = 0 km, IQR = 0 km; females: 0.040 km, IQR = 0–3.38 km; $Z = -1.60$, $P = 0.109$). Except for 2 females (F1 and F4) whose single foraging areas were located more than 2 and 4 km away from the day roost, the majority of individuals had their closest foraging area directly adjacent to their day roost. In commuting between day roost and feeding areas or between the latter, tagged individuals typically did not fly the most direct route, which would have led them through forest, but closely followed the shoreline or flew over open water instead. Some bats (M1, M2, and F1) flew over or crossed only small, forested areas en route to their foraging areas. During commutes along the shoreline, the bats attained a flight speed of approximately 8.3 m/s (30 km/h) as estimated based on the speed of our motorboats (determined by use of a global positioning system unit) while closely tracking a bat.

We estimated nightly flight distances covered by the bats in 2 ways. Based on straight-line measurements between successive point locations, minimum flight distances per night ranged from 3 to almost 18 km. On average, females traveled significantly longer distances (median = 10.74 km, IQR = 9.26–13.33 km) than males (6.42 km, IQR = 4.88–9.05 km; $Z = -3.40$, $P < 0.001$). However, because in reality the bats were often turning and moving back and forth within their foraging areas, a more realistic estimate might be obtained based on average flight speed and nightly flight time. Thus, assuming an average flight speed of 3–4 m/s while foraging (i.e., about one-half of commuting speed) and a mean flight time per night of about 195 min (Weinbeer et al., in press), these bats might travel distances on the order of 35–47 km on a nightly basis. Flight speeds of 3–4 m/s during foraging seem reasonable according to our observations and have also been reported from other bats that hunt over water, for example, *Myotis daubentoni* (Vespertilionidae—Kalko and Schnitzler 1989).

Maximum range span, that is the distance between the day roost and the outermost point of the home range, varied from 0.47 to 7.47 km (measured along the shoreline) and was higher in females (median = 2.97 km, IQR = 2.02–6.09 km) than in males (0.81 km, IQR = 0.55–2.55 km). However, the difference was not statistically significant ($Z = -1.59$, $P = 0.111$). This was probably again due to the fact that range sizes for F3 and F5 could not be fully determined (see above).

Roosting behavior.—All radiotracked bats were captured in the *Barracuda* and most individuals continued to use the ship as their day roost. Intermittent returns to the day roost during the night, sometimes even from distant foraging areas, were common in most individuals with the exception of F4. This female always spent the entire night in its single foraging area and did not fly back to the day roost until approximately 0500 h. All other individuals tracked had multiple night roosts (6 ± 3 roosts, range = 1–10 roosts). Seven of 9 tagged bats used the *Barracuda* for night roosting during some point of their tracking period; 3 individuals (M3, M4, and F3) occasionally roosted in a small shack on nearby Slothia Island. All other night roosts characteristically consisted of earth holes under washed-out roots of trees along the shore of Barro Colorado Island. The bats often revisited the same set of roosts each night, although there was no consistency as to the order in which these visits were made.

Field observations.—Occasionally we were able to follow a bat's flight path with a flashlight by illuminating the reflecting tape attached to the transmitter. Characteristically, the bats foraged at low heights (<50 cm) above the water surface, either flying under or close to overhanging vegetation along the shore but they often also ventured out several tens of meters onto the lake. In general, however, most bats hunted within 50 m from shore. In this context, 1 female (F4) again was a notable exception because examination of our tracking data indicates that this bat periodically foraged at large distances, sometimes as far as 600 m, away from shore out on the lake.

DISCUSSION

Home-Range Size and Patterns of Range Use

Home-range size.—Studies assessing home-range size and patterns of range use in neotropical bats are still few (e.g., Fleming and Heithaus 1986; Gannon and Willig 1997; Handley et al. 1991; Heithaus and Fleming 1978; Kalko et al. 1999; Morrison 1978; Thies 1998; Weinbeer and Kalko 2004). The available information indicates that there is large variation in home-range size among species that is closely linked to spatiotemporal distribution and abundance of food resources and foraging strategies employed, such as foraging in continuous flight versus perch hunting.

Radiotagged *M. macrophyllum* at Barro Colorado Nature Monument occupied small to large home ranges of 7–151 ha, with a median home-range size for all tracked individuals of 24 ha. These values underestimate the true home-range size because at least 2 females could not be followed continuously during all tracking nights. Especially when considering its small body size, it becomes apparent that *M. macrophyllum* has large home ranges compared to other insectivorous phyllostomid bats, a finding that is in contrast to the general trend that small bats have smaller home ranges than larger ones (cf. Fenton 1997). For instance, *Lophostoma silvicolum*, a 34-g, gleaning, insectivorous phyllostomid bat that occurs in sympatry with *M. macrophyllum*, is characterized by small home ranges (mean 17 ha, range 11–31 ha—Kalko et al. 1999) even though it is much larger than *M. macrophyllum*. Small home ranges in *L. silvicolum* mainly reflect a "hang-and-wait" strategy, that is, a rather sedentary foraging behavior. Another sympatric gleaner, the insect- and frog-eating bat *Trachops cirrhosus* (Phyllostomidae), although it is approximately equal in body mass to *L. silvicolum*, has much larger home ranges that are similar in size to those of *M. macrophyllum* (mean 46 ha, range 8–100 ha—Kalko et al. 1999). Although *L. silvicolum* and *T. cirrhosus* both hunt prey from perches in short sally flights, the latter additionally forages for frogs in continuous flight and commutes longer distances (>1 km), leading to larger home ranges compared to *L. silvicolum* (Kalko et al. 1999). These examples show that differences in foraging strategy can have a profound influence on the range over which bats are active.

Another factor that influences home-range size, in addition to foraging mode, is availability and distribution of food in space and time. Small aerial insects, in contrast to, for instance, frogs, which often occur aggregated at spawning pools, are more widely distributed throughout the landscape. Thus, bats like *M. macrophyllum* exploiting this resource should travel longer distances on a nightly basis and have large home ranges. For instance, Weinbeer and Kalko (2004) found average home ranges of 46 ha (range 19–158 ha) for the insectivorous bat *Lampronycteris brachyotis* (Phyllostomidae) on Barro Colorado Island. Similar to *M. macrophyllum* (Weinbeer et al., in press), this species was characterized by a high flight activity of more than 3 h per night, during which the bats traveled estimated distances of several dozen kilometers (*M. macrophyllum*: about 35–50 km, *L. brachyotis*: approximately 60 km), paralleling many aerial insectivorous vespertilionids.

Their high mobility gives bats access to a wide range of habitats and often can liberate them from their dependence on a particular location for foraging (Fenton 1997). Radiotracking studies reveal that bats commute from their roosts to foraging areas over distances of <1 to >20 km (Fenton 1990, 1997); for some species even larger commuting distances have been reported (e.g., up to 50 km for *Leptonycteris curasoae*, Phyllostomidae—Sahley et al. 1993). In this regard, evidence is mounting that distances that can be bridged by a variety of species are not consistent with the proposition that smaller bats should typically fly shorter distances than larger ones. Recent studies have shown that some small species fly remarkably long distances, which in turn results in very large home ranges. For instance, O'Donnell (2001) reported long-distance commutes of up to 19 km for the 10-g temperate rainforest bat *Chalinolobus tuberculatus* (Vespertilionidae) in New Zealand and home ranges that were among the largest known for microbats (median minimum convex polygons 660–1,590 ha, maximum 5,630 ha). Similarly, small (5-g) lesser horseshoe bats, *Rhinolophus hipposideros* (Rhinolophidae), studied by Bontadina et al. (2002) foraged up to 4.2 km from their roosting site and were active over ranges of up to 368 ha. Our data for *M. macrophyllum* likewise fall into that category.

Overall, our results suggest that, even though *M. macrophyllum* employs a gleaning foraging strategy, it more closely resembles aerial insectivorous bats in terms of range size and movement distances (e.g., *Eptesicus serotinus*, Vespertilionidae—Catto et al. 1996; Robinson and Stebbings 1997; *C. tuberculatus*—O'Donnell 2001) than other gleaning insectivorous phyllostomids that forage in and around vegetation (such as the mainly perch-hunting *L. silvicolum*—Kalko et al. 1999).

In the present study, males and females differed considerably in their movement patterns. Female long-legged bats commuted up to 4.5 km from the day roost to their 1st feeding area and 1 female (F5) foraged more than 7.5 km away from the day roost. Long-distance movements can be expected, particularly in bats with high wing loading and high aspect ratio, morphological characteristics that generally confer high aerodynamic efficiency (Norberg and Rayner 1987). However, because wing loading and aspect ratio of *M. macrophyllum* (Weinbeer et al., in press) were well within average values for bats foraging near obstacles low over ground or close to vegetation (e.g., Aldridge and Rautenbach 1987; Norberg and Rayner 1987), they do not appear to be highly adapted to efficiently fly long distances. Nonetheless, distances flown were greater than those recorded for many bats with higher aspect ratios and wing loading (e.g., *Megaderma lyra*, Megadermatidae—Audet et al. 1991; *E. serotinus*—Catto et al. 1996; *Noctilio albiventris*, Noctilionidae—Fenton et al. 1993; compare to Fenton 1990, 1997). For species such as *M. macrophyllum* that often fly close to water surfaces, the effect of increasing flight costs with lower-aspect-ratio wings could be mitigated by the aerodynamic "ground effect," which can represent a reduction in induced drag of about 10% because of the proximity of the wing aerofoil to the water surface (Norberg and Rayner 1987). Roosting in groups or colonies can have important implications for foraging movements and the spacing behavior of individuals. According to refuging theory (Hamilton and Watt 1970), individuals of colonial species should undertake long commuting flights to reach food resources not depleted or dominated by conspecifics in order to reduce intraspecific competition. For instance, the highly gregarious southern long-nosed bat (*L. curasoae*), commutes distances of 15–50 km to its feeding areas (Horner et al. 1998; Sahley et al. 1993). In contrast, solitary bats or species that live in small colonies usually incur minimal time and energy costs for commuting, although this often may be above all a consequence of their respective foraging strategy (e.g., Bonaccorso et al. 2002; Kalko et al. 1999; Winkelmann et al. 2000). Interestingly, in the present study, distances moved and home ranges were largest in the 2 postlactating females, F4 and F5. Range expansion in postlactating females also has been documented in other bats and has been interpreted as a mechanism to avoid competition with newly volant young (Clark et al. 1993; O'Donnell 2001). O'Donnell (2001) argued that while flight capabilities of juveniles are not yet fully developed, there will be considerable use of resources close to the day roost. It should therefore be advantageous for adults to move to more distant foraging areas, which would potentially reduce competition with juveniles at that particular time. Colony size in the day roost had roughly doubled after the birth peak in mid-May and tracking of the 2 females coincided with a large number (approximately 50) of newly volant juveniles.

The larger range spans observed in females as opposed to males might, at least in part, be explained by increased energy demands and nutritional requirements linked to the reproductive status of the females, which might have forced them to forage over a wider range.

We are aware of the fact that, with only 9 individuals tracked over just 1 season, our database is limited and as such our results should not be taken to constitute a definitive account of the foraging and ranging behavior of *M. macrophyllum*. However, we believe that our data adequately characterize the bats' general foraging behavior, that is, hunting exclusively over water. Likewise, other than some differences associated with reproductive cycle and social status, we do not expect profound seasonal changes in the ranges over which *M. macrophyllum* is active.

Use of foraging and core areas.—Although overall ranges were large, *M. macrophyllum* concentrated its activity in small core-use areas of typically less than 10 ha, representing roughly 35% of the size of foraging areas. There was moderate spatial overlap between foraging and core areas of individual bats (Fig. 2). However, because we were only able to track 1 bat at a time, we could not test whether there was also temporal overlap in the use of feeding sites.

Individual bats typically used the same foraging areas on successive tracking nights, a pattern in agreement with other studies of insectivorous bats (e.g., Entwistle et al. 1996; Wai-Ping and Fenton 1989). Many bat species appear to have detailed knowledge of habitat patches in their range with high prey availability, and therefore may maximize food intake by preferentially feeding in such sites (Entwistle et al. 1996). This is a likely explanation for the highly predictable foraging behavior and space use shown by F4, which contrasted in many ways with the patterns observed in the other individuals tracked. After emergence from the day roost, this female commuted about 4.5 km each night to its single feeding area at Harvard Peninsula (Fig. 2e), where it stayed the entire night. Throughout the tracking period it used only 1 night roost from which it made several foraging flights in the course of the night. However, it not only foraged close to the shore as was usual with the other individuals but often made forays of up to 600 m onto the lake. This idiosyncratic behavior might reflect a response to a particularly profitable resource patch, such as presence of large numbers of floating *Hydrilla verticillata* (Hydrocharitaceae) associated with large numbers of insects (particularly the pyralid moth *Parapoynx diminutalis*—Weinbeer et al., in press) on these aquatic plants.

Influence of social status on range use.—Examination of our data suggests a polygynous, harem-forming mode of social organization for *M. macrophyllum*, a mating system that has been documented for various other phyllostomids such as *Artibeus jamaicensis* and *Carollia perspicillata* (Fleming 1988; Ortega and Arita 1999). Foraging movements of males appeared to be sensitive to their social status. The harem male (M3) we tracked restricted its foraging activity to a very small area around the day roost, most likely to be able to allocate more time to roost vigilance and female defense. The other males had feeding areas at various distances away from the day roost but in general they also foraged closer to it than did females. Having ranges closer to the day roost might be the best option for these males if they want to increase their chances to gain access to females in the day roost and attempt sneak matings.

Night-roosting behavior.—Radiotracked *M. macrophyllum* commonly used several night roosts throughout their tracking period. Night roosts may serve as resting places between foraging bouts, a behavior that is common in insectivorous bats (Entwistle et al. 1996; Weinbeer and Kalko 2004) and one that we also observed in *M. macrophyllum*. Kunz (1982) postulated that night roosts should be located close to foraging sites to avoid costly commutes to day roosts and minimize predation risk. This is in part corroborated by our observations of *M. macrophyllum*. During the night, the majority of individuals roosted in hollows under washed-out roots of trees or in overhanging vegetation along the lakeshore. These night roosts were always located on the periphery of foraging areas. However, flights back and forth between day roost and foraging areas during the night were also common in most individuals of tracked *M. macrophyllum*. It is well known that maternity roosts are commonly used as night roosts by lactating females, which reflects the need to suckle their young (e.g., Anthony and Kunz 1977; Kunz 1982). On the other hand, it remains largely speculative why nonreproductive females should make long and apparently costly flights back to the roost during the night, as was the case in this study. For some species, it has been proposed that these intermittent returns might be related to a lower risk of predation at the day roost (Fleming and Heithaus 1986; Thies 1998). However, this implies that these flights are less costly in terms of energy expenditure and exposure to predators than the use of night roosts that are located close to a bat's feeding area. It can be assumed that night roosts as described above represent safe roosting sites for *M. macrophyllum* so it is not readily apparent why the bats undertake these flights to the day roost and back. Judging from their ability to travel these distances in moderately fast flight, such commutes may in fact not be as energetically costly as it might 1st appear. This is also suggested by the long cumulative distances that *M. macrophyllum* moved on a nightly basis, which were much greater (>35 km) than commutes between day roost and foraging sites. We do not know whether night roosts are shared by several individuals, and if so, to what extent social interactions in these roosts occur. But perhaps realization of mating opportunities might only be possible in the day roost. Therefore, these intermittent returns may be best explained by increased social activity in the day roost associated with the onset of the reproductive phase.

Habitat Use in Relation to Other Species

The air above bodies of water was identified as the key habitat used by foraging *M. macrophyllum*. Aquatic habitats are generally rich in insects and therefore provide attractive feeding opportunities for a variety of bat species (Rydell et al. 1999; Siemers et al. 2001). In the study area, 5 species characteristically forage over water. In addition to *M. macrophyllum*, this foraging habitat is also used by the 2 species of bulldog bats (*Noctilio leporinus* and *N. albiventris*), 1 emballonurid (*Rhynchonycteris naso*), and 1 member of the Vespertilionidae (*Myotis albescens*—Kalko et al. 1996). Except for *N. leporinus*, which is well known for its fish-eating habits but also includes insects in its diet (Brooke 1994; Schnitzler et al. 1994), all of these species are insectivorous. *R. naso* and *M. albescens* are both aerial insectivores and gleaners, catching their prey on the wing above water and taking it directly from the water surface. Similar to *M. macrophyllum*, the 2 species of *Noctilio* catch their prey either in trawling mode from the water surface or capture insects emerging from or swarming over their aquatic habitat in the air (Brooke 1997; Hood and Pitocchelli 1983; Schnitzler et al. 1994). Taken together, all 5 species show high flexibility in hunting strategies. Overall, they differ considerably in body size and mass (*R. naso*, 3.4 g; *M. albescens*, 6.5 g; *M. macrophyllum*, 8.4 g; *N. albiventris*, 30.7 g; and *N. leporinus*, 55.3 g—Kalko et al. 1996). They can therefore also be assumed to select prey of different sizes. Generally, larger bats have access to large and small prey, whereas smaller bats are limited to small prey items (e.g., Aldridge and Rautenbach 1987; Fenton 1990). Size-related spacing along the resource axis could hence be a mechanism for reducing potential competition for food. However, this implies that insects indeed constitute a limiting resource, an assumption that remains to be tested. Unfortunately, apart from differences in foraging modes, comparative data are lacking to evaluate whether and how the 5 species differ with respect to patterns of range use in space and time to further facilitate coexistence. Basset (1995) argued that coexistence between interspecific competitors should also be possible even under complete niche overlap because of body size-related spatiotemporal constraints imposed on home-range resource exploitation. He proposed that size-related inefficiency in home-range exploitation should generate a size-structured guild and community organization, a scenario that could be envisaged for the bat species that forage over water in our study area.

Conclusions

The foraging behavior of *M. macrophyllum* differs in a unique way from that of other phyllostomid bats in that it forages over water, gleaning insects from the water surface similar to noctilionid bats, some vespertilionids, and the emballonurid *R. naso*.

Despite its small size, *M. macrophyllum* was active over remarkably large ranges. Our findings hence do not support a general positive correlation between home-range size and body size in bats. Home-range size and spacing patterns of *M. macrophyllum* to a large degree reflect the bats' foraging strategy, diet, and dispersion of food resources. We conclude that these factors, rather than body size, are the chief determinants and best predictors of home-range size. Life-history dynamics such as reproduction as well as intraspecific competition linked to colony size or social status further modify spacing behavior and movement patterns of individuals, resulting in marked interindividual and gender-specific differences and variability in observed home-range sizes.

RESUMEN

Usando telemetría estudiamos el tamaño de rango de hogar y patrones de uso de rango de 4 machos y 5 hembras del murciélago *Macrophyllum macrophyllum* (Phyllostomidae) en el Monumento Natural Barro Colorado, Panamá, entre abril y julio 2002. *M. macrophyllum* forrajeó en áreas extensas comparado con otros filostómidos de tamaño similar. La mediana de tamaño de rango de hogar para los 9 individuos era 23.9 ha (7.3–150.7 ha). Con una mediana de 17.3 ha (7.3–24.9 ha), los rangos de hogar de machos eran algo, pero no significativamente, más pequeños que en hembras (44.4 ha, 16.3–150.7 ha). Los murciélagos forrajearon exclusivamente sobre agua, cazando cerca de la orilla del Lago Gatún. Las áreas de forrajeo variaban entre 2.7 y 96.1 ha, con una mediana de 12.3 ha para ambos sexos. En general, había alta consistencia de noche a noche en cuanto al uso de áreas de forrajeo. La mayoría de los individuos tenía múltiples áreas de forrajeo y áreas núcleos. Las áreas núcleos correspondieron a aproximadamente 35% de las áreas de forrajeo y eran más grandes en hembras (mediana = 5.3 ha, 1.1–54.1 ha) que en machos (3.3 ha, 2.6–8.7 ha). La extensión máxima de rango varió de 0.5 a 7.5 km; los machos en general y especialmente un macho del harén forrajearon mucho más cerca de su refugio diurno que las hembras. *M. macrophyllum* viajó unos estimados 35–47 km durante su período de actividad nocturna y las distancias de vuelo eran significativamente más grandes en hembras que en machos. Nuestros resultados no proporcionan apoyo para la proposición que murciélagos pequeños típicamente tienen rangos pequeños de hogar. Al contrario, concluimos que la estrategia de forrajeo, dieta, dispersión de recursos de alimento, y la morfología del ala generalmente son mejores determinantes del tamaño de ámbito de hogar. Además, la condición reproductiva, así como la competencia intraespecífica relacionada con el tamaño de la colonia o el estatus social también afectan el uso de espacio y patrones de movimiento de éstos murciélagos. Aunque *M. macrophyllum* emplee una estrategia de forrajeo típica de murciélagos insectívoros de follaje ("gleaners") nuestros resultados sugieren una semejanza profunda a murciélagos insectívoros aéreos en cuanto al tamaño de rango de hogar y las distancias de movimiento.

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