

FORAGING STRATEGY AND BREEDING CONSTRAINTS OF *RHINOPHYLLA PUMILIO* (PHYLLOSTOMIDAE) IN THE AMAZON LOWLANDS

MICKAËL HENRY AND ELISABETH K. V. KALKO*

Département d'Ecologie et Gestion de la Biodiversité, CNRS/MNHN–UMR 5176, 4, Avenue du Petit Château, F-91800 Brunoy, France (MH)

University of Ulm, Department of Experimental Ecology, Albert-Einstein Allee 11, D-89069 Ulm, Germany (EKVK)

Smithsonian Tropical Research Institute, Balboa, Republic of Panama (EKVK)

Bat diversity peaks in neotropical lowland forests, where 70–100 species may coexist in local assemblages. Understanding of factors that promote and maintain this diversity requires a thorough knowledge of the ecology and behavior of individual species. We studied the movement pattern, focusing on range size and foraging strategy, of the small frugivorous bat *Rhinophylla pumilio* (Phyllostomidae), with particular emphasis on constraints females have to deal with when rearing young. Because of the scattered distribution of its main food resource, infructescences of epiphytes, we hypothesized that *R. pumilio* should spend most of its flight time searching for food. Because its small body size incurs higher flight costs in comparison to larger fruit-eating bats, we further proposed that it should feed within small foraging areas that are close to each other and that commuting flights between foraging areas should be short and infrequent, resulting in small home ranges. Furthermore, we predicted that lactating females would change range size as well as activity budget by performing more search flights to increase food intake for milk production and more commuting flights to feed their young during nighttime. We radiotracked 9 females (4 nonreproductive, 4 lactating, and 1 subadult) and 2 males in the primary rain forest of Nouragues, French Guiana, for a total of 49 nights. Supporting our initial prediction, the foraging strategy of *R. pumilio* was mostly restricted to short (40- to 120-m) search flights in a single, rather small foraging area (3.5–14.1 ha). We observed a decrease in flight distances and size of foraging area, and an increase in total flight time throughout the night in lactating females that probably transported their young and nursed them in their foraging areas at night. Finally, we propose that the sensitivity of *R. pumilio* to forest fragmentation reported in previous studies may in part be caused by its foraging strategy because it consists mostly of short-distance search flights that make it difficult or impossible, particularly for lactating females, to regularly cross broad expanses of inhospitable matrix in fragmented forests. Fragmentation may therefore decrease breeding success and foster population decline in this species.

Key words: activity pattern, breeding behavior, foraging activity, French Guiana, fruit bat, lactation, Phyllostomidae, *Rhinophylla pumilio*

Bat diversity and abundance peaks in neotropical lowland forests, where 70–100 species may coexist (e.g., Lim and Engstrom 2001; Simmons and Voss 1998; Voss and Emmons 1996). A thorough knowledge of mechanisms that promote and maintain this high diversity is crucial because of the contributions of bats to key ecological processes such as seed dispersal, pollination, and predation (e.g., Charles-Dominique

1986; Kalka and Kalko 2006; von Helversen and Winter 2003). Partitioning of resources in space and time is seen as one of the main factors facilitating coexistence within bat assemblages (e.g., Arita 1997; Bonaccorso 1979; Delaval et al. 2005; Fleming et al. 1972; Kalko et al. 1996).

Autecological data also are of particular relevance for conservation with regard to habitat disturbance and fragmentation affecting species assemblages as well as individual species. Although overall species richness of bats tends to decrease in habitats that are reduced to small, isolated fragments (Cosson et al. 1999; Estrada and Coates-Estrada 2001, 2002; Estrada et al. 1993; Schulze et al. 2000), some species tolerate fragmented habitats better than others

* Correspondent: elisabeth.kalko@uni-ulm.de

(e.g., Brosset et al. 1996; Gorresen and Willig 2004; Kalko 1998; Schulze et al. 2000). Identifying life history traits that make some species more prone than others to decline or go extinct requires a thorough knowledge of the bats' ecology and behavior. However, because of their nocturnal habits and high mobility, detailed knowledge is still scarce for most species. This is particularly true for movement patterns, that is, the manner in which bats move across a landscape to search for and exploit resources.

Published telemetry data of neotropical bats are restricted to a few species (e.g., Kalko et al. 1999; Meyer et al. 2005; Weinbeer and Kalko 2004; Weinbeer et al. 2006), encompassing fruit-eating bats, namely the large *Artibeus jamaicensis* (Handley and Morrison 1991; Morrisson 1978a, 1978b), and the medium-sized *Carollia perspicillata* (Charles-Dominique 1991; Heithaus and Fleming 1978), *C. castanea* (Thies and Kalko 2004; Thies et al. 2006), and *Stenoderma rufum* (Gannon and Willig 1997). *A. jamaicensis* and *C. perspicillata* have become reference models to illustrate differences in foraging strategies in the context of resource availability. On one hand, large bats of the genus *Artibeus*, typically specialize on mass-producing (big-bang) crops, particularly figs (*Ficus* spp., Moraceae), often require long (>2–10 km) commuting distances and several shifts in foraging area per night, whereas medium-sized bats of the genus *Carollia* specialize on the steady-state crops of the understory shrubs *Piper*, *Solanum*, and *Vismia* that permit smaller home ranges with fewer shifts and usually shorter commuting distances (<1–2 km) per night.

We examined the movement patterns of the small (9-g) *Rhinophylla pumilio* (Phyllostomidae) that is widespread across Amazonian forests and the Guiana Shield. Our objective was to document range size and foraging strategy of *R. pumilio* in an undisturbed rain forest with special emphasis on physiological constraints faced by females when rearing young. *R. pumilio* is highly specialized for eating infructescences produced by epiphytic Araceae and *Philodendron* spp., Cyclanthaceae (e.g., Cockle 1997; Cosson 1994; Delaval et al. 2005). These epiphytes are widely scattered in the forest, occurring on up to 80% of tree trunks at about 1–8 m aboveground (Cockle 1997, 2001; M. Henry, in litt.). They produce a few or only a single infructescence at a time. The spatiotemporal distribution of the epiphyte fruit resource shares more characteristics with shrubs (steady-state crops with spatially scattered fruits) than with fig trees (big-bang crops with locally abundant fruits). Therefore, we hypothesized that, similar to the shrub frugivores *C. perspicillata* and *C. castanea*, the foraging strategy of *R. pumilio* would rely on frequent search flights and less on commuting flights between foraging areas. Accordingly, *R. pumilio* should use few foraging areas and these should be close to each other and form a relatively small home range whose size and location should be more stable over time than, for example, that of the large fruit-eating bat *A. jamaicensis*.

Range size also may be influenced by body size and the peculiar roosting behavior of *R. pumilio*, where individuals roost alone or in small groups under leaves of epiphytes or large palm fronds modified into tents (Charles-Dominique 1993; Simmons and Voss 1998). Small body size incurs higher

flight costs and is likely to limit home-range size compared to larger fruit-eating bats. The low roost fidelity observed in tent-roosting bats compared to species roosting in caves or hollow trees suggests frequent shifts between roosts, most likely to minimize commuting distances between day roosts and foraging areas (Lewis 1995).

Furthermore, we argue that the physiological constraints of rearing a young may force females to modify their movement pattern, as has been previously suggested for *C. perspicillata* (Charles-Dominique 1991) and for a range of insectivorous bats (e.g., Henry et al. 2002; Kurta et al. 1989; Racey and Swift 1985; Swift 1980). Indeed, as typical "income breeders," female bats rely on current food intake to support costs of reproduction and require high food intake to meet the demands of milk production. For example, the energetic requirements of *C. perspicillata* increased by 1.5–2 times during lactation (Fleming 1988). A higher energy intake can be achieved by conducting more search flights in order to harvest more fruits in a given foraging area. At the same time, the need to feed young during the night may force females to decrease the length or frequency of commuting flights between foraging areas.

Finally, because *R. pumilio* has been classified as fragmentation-sensitive (Cosson et al. 1999), we discuss whether limitations in range use combined with breeding constraints are likely to contribute to its decline in recently fragmented areas.

MATERIALS AND METHODS

Study site.—The study was carried out at the Nouragues research station in the center of the Réserve Naturelle des Nouragues, northern French Guiana (4°50'N, 52°42'W; 80–110 m above sea level). Nouragues is part of a large block of continuous tropical lowland rain forest where human influence has been negligible over the past 2 centuries (Charles-Dominique 2001). Annual temperature averages 26.3°C. Total annual rainfall amounts to 2,500–3,200 mm with mean monthly rainfall of 250 mm (Grimaldi and Riéra 2001; P. Charles-Dominique, pers. comm.). There is a marked dry season from August to November with only 16% of total annual rainfall. Trees of the families Caesalpiniaceae, Sapotaceae, and Lecythidaceae dominate the canopy (Poncey et al. 2001).

Bat captures and radiotracking.—We followed guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998) in our procedures. All *R. pumilio* were captured with groups of three 12-m mist nets (height 2.5 m, 4 shelves) set in a T-pattern and moved each night within a 300 × 400-m area transected by a 5-m-wide creek, and located in the middle of the 100-ha Nouragues research station quadrat, which is covered by a 100-m-spacing grid of forest trails. Captured bats were temporarily kept in cloth bags and released at the study site. Reproductive status of females (pregnant, lactating, or nonreproductive) was assessed by checking for the presence of a palpable fetus or prominent hairless nipples (Racey 1988). Juveniles and subadults were distinguished from adults based on the degree of fusion of metacarpal epiphyses (Anthony 1988). Individuals were weighed with an electronic

scale (Ohaus Corporation, Pine Brook, New Jersey) to the nearest 0.1 g. Only bats >8.5 g were radiotracked. Eleven individuals were selected for radiotracking, including 4 nonreproductive females (F1–F4) and 4 lactating females (F5–F8), 1 subadult female (F9), and 2 nonreproductive males (M1 and M2). The transmitters (0.70 g; Biotrack Ltd., Wareham, Dorset, United Kingdom) represented $6.9 \pm 0.9\%$ *SD* of the bats' body mass, which slightly exceeds the recommended 5% (Aldridge and Brigham 1988). We attached the transmitters with cyanoacrylate glue (Henkel France SA, Boulogne-Billancourt, France) to the interscapular region of the bats after trimming the fur. No lesions were found on recaptured bats, neither in the short term (4 to 45 days, $n = 4$) nor medium term (5 and 12 months, $n = 2$) after tagging.

Bats fitted with a transmitter were fed with sugar water and released at the capture site within 1 h. We radiotracked 1 bat at a time, using an FT-290R receiver (YAESU Electronics, Cypress, California) and a 4-element Yagi antenna (Tonna Electronics, Mondelange, France). All tracking sessions were conducted in the middle of the wet season between February and May in 2003 and 2004, except for M1, which was tracked in October 2003 (dry season). M2 was fitted with a 0.84-g position-sensitive transmitter (9.7% of body mass; model LB-2B; Holohil Systems Ltd., Carp, Ontario, Canada) where a mercury switch modulated pulse rhythm according to its inclination with a high repetition rate when the bat was flying and a slower rate when the bat was hanging. Lactating female F5 was caught together with a volant juvenile that must have been her own because she fed it in the capture bag. They were released together. Bats were tracked for 5 consecutive nights unless the transmitter fell off sooner ($n = 4$). Bats were not tracked during the night of release because they may have been stressed after handling. No tracking session was undertaken during the 6-day period encompassing full moon because of possible bias induced by lunar-phobia.

We determined temporary hanging locations of the tagged bats at night using triangulation based on 2 bearings. Bearings were taken following the direction of maximal signal intensity according to the receiver intensity gauge. We constantly moved along trails, either alone or with 2 persons who stayed in radio contact, to follow the bat as closely as possible. Bats were considered hanging when the transmitter signal was judged constant in direction and intensity for at least 1 min. We occasionally failed to locate hanging phases shorter than 2 min because we could not reach adequate tracking positions in this short period of time.

The precision of our triangulation depended on the distance between the transmitter and the receivers and on the angle between bearings. To assess the resolution of our equipment, we took bearings in the forest understory from 65 positions 15–195 m from a transmitter placed 2 m above ground level. Triangulation error (distance error between bearing intersection and real location of transmitter) rarely exceeded ± 15 m. Furthermore, the rather flat terrain and the accurate 100-m spacing grid of forest trails marked every 10 m ensured that each pair of bearings formed an adequate angle for triangulation (20–160°).

Coordinates of the tracking positions, mostly at trail intersections, were obtained from a custom-made map of the study site, based on a 1/50,000 map (Institut Géographique National, France, and digitized by P. Charles-Dominique) using "Corel Designer" 4.1 (2) (MicrografX, Corel Corporation, Neuilly-sur-Seine, France). The fixes, that is, bat hanging locations, were analyzed using the software Tracker 1.1 (1994, Camponotus AB, Solna, Sweden). All fixes exceeding maximum detection range around bearing positions (>350 m) were discarded before analyses. These accounted for only 1.5% of total fixes.

Data collection.—To avoid any influence of day-roost locations on estimations of foraging areas, we restricted analyses of foraging strategy to the time interval 1915 h to 0615 h and discarded data recorded during the approximately 25-min period after dusk-emergence from and before dawn-return to the day roosts. We continuously monitored the bats' activity by noting time (rounded to the nearest minute) for each transition between flight and hanging phases, and between loss and retrieval of signals. Bearings were taken for each hanging phase until midnight. We also located the position of day roosts every day for each tracked bat following the direction of the radiosignal until we were close (<20 m) based on signal intensity. We then searched the surrounding vegetation until we found the roost. For comparison, we characterized 2 main aspects of movement patterns: range size, in particular home range, foraging areas, and core areas as well as foraging strategy, namely use of search and commuting flights. Furthermore, we evaluated activity rhythm of individual bats over the night in relation to female reproductive status.

Range size.—We used size of home range, foraging area, and core area to characterize the spatial extent of the habitat that the bats used in the forest with regard to their activities devoted to roosting and foraging including searching for food, consumption, and digestion during the night. Type and duration of activities were estimated for each individual from all of its tracking locations gathered during day and night within the 5-day sessions. We used the 100% minimum convex polygon method to define the home range that comprised both roosting and foraging activity. Minimum convex polygon is a method that connects the outermost fixes to delineate a single area enclosing all fixes. In contrast, foraging areas and core areas were restricted to a single type of activity (i.e., foraging activity) and were analyzed using the probabilistic kernel method (adaptive Gauss method, density $CV = 0.15$ —Worton 1989). This method lays out isopleths that delineate zones of equal probability of presence of tracked individuals. Foraging areas refer to the entire area encompassed during foraging activity, whereas core areas were defined as preferred zones within foraging areas. To permit comparisons with other studies on phyllostomids (e.g., Thies et al. 2006), we defined foraging areas and core areas as the surfaces enclosing 95% and 50%, respectively, of the probability of presence of the bats.

To minimize temporal autocorrelation (Worton 1989), we choose longer time intervals between localizations than the time a bat would require to cross its home range. We localized

bats only once during hanging phases so that time intervals were not standardized but depended on duration of flights between hanging phases. Because these intervals mostly exceeded 3–4 min, this was enough for a bat to commute across its home range (see “Results”).

The fixes used to estimate foraging areas and core areas represent the location of bats hanging in temporary night roosts and of feeding phases on epiphyte infructescences. Because the infructescences are too large to be removed by *R. pumilio*, the bats land on them and consume part of the pulp of the ripe fruit in situ including small tiny seeds (Cockle 1997). This contrasts with other fruit-eating bats that carry fruits such as figs, fruiting spikes of *Piper*, or berries of *Solanum* to temporary feeding roosts for processing (Fleming 1981; Morrison 1978a).

Foraging strategy.—To distinguish between types of flights and to assess their relative frequency during foraging activity, we discriminated between flights within a single foraging area as search flights and flights between 2 foraging areas as commuting flights. Additionally, we also established a quantitative definition of search and commuting flights. For search flights, we assumed that the bats were flying at low flight speed in the foraging area searching for food. For commuting flights, flight speed should be higher when individuals fly straight from one locality to the next. We computed mean flight speed of all flights (linear flight distance between successive hanging locations divided by flight duration) and classified all flights ≤ 3 m/s as search flights. This conservative approach was based on other studies revealing average flight speeds of 4–8 m/s for direct commutes between day roost and (1st) foraging area (Heithaus and Fleming 1978; Weinbeer and Kalko 2004). Given the spatial (± 15 m) and temporal (± 1 min) resolution of our tracking survey, we were able to discriminate between commuting and search flights among hanging locations located >250 m apart.

Effect of reproductive status on movement patterns.—Some bats transport their young while foraging (Kunz and Hood 2000) to where the mothers are likely to return at night to regularly feed their young. We wanted to know whether lactating *R. pumilio* also show this behavior, and how this may in turn modify the general movement patterns of *R. pumilio*. We therefore checked, whenever possible, for the presence of a young remaining in a day roost after the emergence of a tracked, lactating bat, using a low-intensity diffuse white light (Tikka LED headlamp; Petzl, Crolles, France). We also assessed from our tracking data whether lactating bats frequently returned to a specific hanging location within their foraging areas. This could indicate shuttling flights between foraging areas and a night roost. Assuming that 2 hanging locations were potentially the same when they were situated <15 m apart (i.e., within the estimated upper limit of the error occurring for fixes), we defined an index of revisitation rate to hanging locations, calculated as the ratio $[(\text{total no. hanging phases} - \text{no. distinct hanging locations}) / (\text{total no. hanging phases} - 1)]$. These values, computed for each night, range from 0% (all hanging phases were at different locations) to 100% (all hanging phases were at the same location). They were arcsine-transformed and compared between reproductive

groups (nonreproductive versus lactating females) using a nested analysis of variance (ANOVA).

We analyzed the effect of reproductive status on home-range size, size and number of foraging areas and core areas, distances between day roosts and nearest foraging areas, flight distances, foraging strategy, particularly proportions of search and commuting flights, and activity rhythm across the night encompassing cumulative flight time per night, and duration and frequency of flights and hanging phases. When an individual bat used more than 1 foraging area or core area, areas were pooled. To compare differences in flight times over the night, we 1st calculated the time each bat spent flying in 30-min intervals for the whole tracking night (1915 h to 0615 h). We then performed a 2-way repeated-measure ANOVA to assess possible fluctuations in time spent in flight across the night intervals and between reproductive groups. This analysis was performed separately for the 2 parts of the night, before and after 0030 h. For the other parameters of movement pattern, we used either Student's *t*-test (range sizes and distance between day roosts and foraging areas) or a nested ANOVA when many values were assigned to each bat, including flight distances, duration of flights and of hanging phases, number of hanging phases per hour, and revisitation rate of hanging locations. When necessary, the latter variables were log- or square-root-transformed to establish normality before comparison. Departures from normality were assessed using Kolmogorov–Smirnov tests. All statistical tests were performed using Systat 9.0 (SPSS Inc., Chicago, Illinois).

RESULTS

Range size.—We obtained a total of 529 fixes during 42 full tracking nights (11 h each) for the 9 females and 7 half tracking nights (5 h each) for the 2 males. Periods where we lost the signal and other interruptions such as bad weather rarely exceeded 20 min and accounted for only 2.7% of total tracking time. We successfully located all day roosts of the tagged animals. The 23 roosts were situated within the 100-ha quadrat centered on the research station and all but 3 could be visually identified. Six roosts were under large leaves of epiphytes (*Philodendron fragrantissimum* and *P. ornatum*, Araceae) and 7 were under young fronds of juvenile palms (*Astrocaryum sciophilum*, Arecaceae). All of the *Philodendron* leaves were modified into tents, with chewed veins along the central vein, whereas 4 (57%) *A. sciophilum* leaves remained unmodified. In 4 cases, bats were found under large unmodified mature leaves of young *Jessenia bataua* (Arecaceae) and twice under unmodified dry leaves of *Cecropia sciadophylla* (Cecropiaceae) that formed an umbrellalike shelter. All identified day roosts were situated 1–4 m above ground.

Sizes of home ranges and foraging areas were rather small and varied from 2.5 to 16.9 ha and from 3.5 to 14.1 ha, respectively (Table 1). Each bat used a single foraging area. Flights that extended far beyond the limits of the foraging areas where we typically lost signal contact were rare given the exceptionally high overall contact time of 94–100% throughout

the study. Foraging areas enclosed 1–3 small core areas totaling 0.5–2.4 ha (Fig. 1; Table 1). Although we obtained relatively few fixes per bat (47.3 ± 12.3 SD), cumulative values of home-range size (day roosts excluded) of most individuals tended to reach a plateau after 30 fixes were included in the analysis (Fig. 2), indicating that the spatial range of their nocturnal activity was well described.

Contrary to our prediction, bats mostly used day roosts located outside of their foraging area (15 of 27 day roosts). Accordingly, home ranges calculated by the minimum convex polygon method averaged 81% larger than foraging areas (range 5–242%; Table 1). The distance between day roosts and foraging areas averaged $101 \text{ m} \pm 140$ SD when attributing a nil distance to roosts situated inside foraging areas, and 212 ± 146 m when considering only roosts outside of foraging areas. Tracked bats rarely roosted alone (5 times of 40 observations) and group size typically ranged from 3 to 7 individuals.

Foraging strategy.—Because all tracked individuals used a single foraging area each, none of the 420 recorded flights matched our definition of commuting flights as flights between 2 foraging areas. As further support for the prevalence of search flights over commuting flights, we could identify in our database only 2 long, straight flights attaining mean speed of ≥ 3 m/s. These were 400-m-long flights performed at a speed of 3.3 m/s. As much as 98.3% of the flights had an average flight speed of less than 1 m/s. Therefore, we regarded virtually all flights as search flights.

Effect of reproductive status on movement pattern.—Lactating females took their pups when emerging from day roosts at dusk right away ($n = 8$) or after a maximum of only 10–12 min ($n = 2$). Furthermore, during the night, lactating females exhibited a higher revisitation rate to hanging locations than nonreproductive females (28% and 18%, respectively; Tables 1 and 2), indicating the possibility of regular returns to particular night roost(s) for nursing. Compared to nonreproductive females, lactating *R. pumilio* displayed significantly smaller foraging areas (-42% , $t = 4.08$, $d.f. = 5.4$, $P = 0.01$) and shorter flight distances (-25% ; Table 2). However, neither the size of core areas ($t = 2.24$, $d.f. = 3.1$, $P = 0.11$) nor the size of home ranges ($t = 1.44$, $d.f. = 4.4$, $P = 0.21$) was affected by reproductive status. We did not find a significant link between female reproductive status and roosting behavior. As for the other females, lactating females roosted in a wide variety of plants, they displayed a low roost fidelity and changed roosts on average every 2nd day (Table 1). They did not shorten distances between day roosts and foraging area ($t = 1.52$, $d.f. = 20$, $P = 0.14$).

The typical activity rhythm of nonreproductive adult males and females was characterized by alternations of medium-long flights (10–15 min) and somewhat longer hanging phases (15–20 min; Table 1). Long hanging phases (1–2 h) were occasionally observed, mostly during the 2nd part of night. Two-way repeated-measures ANOVAs revealed significant differences in the pattern of nightly activity rhythm (flight time per 30-min interval; Fig. 3A) between reproductive groups, depending on the part of night and the reproductive status of bats. Before 0030 h, flight time varied among the 11 time

intervals ($n = 23$ cases with no missing data, $F = 7.60$, $d.f. = 10, 12$, $P < 0.001$) and a significant interaction occurred between the time intervals and reproductive status ($F = 3.13$, $d.f. = 10, 12$, $P = 0.032$), but no effect of reproductive status alone was detected ($F = 1.27$, $d.f. = 1, 21$, $P = 0.270$). After midnight, flight time varied by reproductive status ($n = 28$ cases with no missing data, $F = 8.10$, $d.f. = 1, 26$, $P = 0.009$), but did not vary among the 11 intervals ($F = 1.11$, $d.f. = 10, 17$, $P = 0.41$), and no interaction between reproductive status and time interval was detected ($F = 1.29$, $d.f. = 10, 17$, $P = 0.31$, respectively). Although activity was rather even after midnight, lactating females spent significantly more time in flight than did nonreproductive females (Fig. 3A). This resulted in a fairly linear cumulative flight time for lactating females that remained steeper than that of nonreproductive females after midnight (Fig. 3B). By the end of the night, cumulative flight time of lactating females differed significantly from that of nonreproductive females and was on average 42 min (20.0%) longer (Table 2).

Neither duration nor number of flights and hanging phases varied from the 1st to the 2nd part of night for lactating females (Fig. 4). In contrast, the general decline in flight time of nonreproductive females during the 2nd part of night (Fig. 3) was associated with a marked increase of the mean duration of hanging phases (Figs. 4B), and thus fewer hanging phases per hour (Fig. 4C). In nonreproductive females, 13.9% of hanging phases lasted more than 1 h, in contrast to only 1.1% for lactating females. The 2 significant interactions between reproduction status and part of night (Table 2) support the observations that nonreproductive females increased their hanging time during the 2nd half of night with several long hanging phases (>1 h), whereas lactating females maintained a high activity level all night long by alternating short flights and hanging phases (14 and 22 min, respectively).

A 2nd trend was the significant increase of mean duration of flights for lactating females (Fig. 4A; Table 2) compared to nonreproductive females. They flew 2.2–4.3 min (18–46%) longer than nonreproductive females between 2 consecutive hanging phases. Finally, the effect of reproductive status on the duration of hanging phases was not significant (Table 2), but although duration of hanging phases increased for nonreproductive females after midnight, it remained unchanged for lactating females, as indicated by the significant interaction of hanging phase duration with the part of night. Limiting the analysis to the first 2 h of the night, when activity peaked simultaneously in both reproductive groups (Fig. 3A) and was probably mostly devoted to food intake, revealed significant differences regarding flight time and hanging phases. Flight time and hanging phases of lactating females were 5–6 min longer than those of nonlactating females. Nonreproductive and lactating females flew $8.7 \text{ min} \pm 5.3$ SD and 13.7 ± 8.1 min, respectively (nested ANOVA; $n = 141$; effect of reproductive status: $F = 19.12$, $d.f. = 1, 131$, $P < 0.001$; effect of individuals: $F = 1.51$, $d.f. = 6, 131$, $P > 0.05$; $R^2 = 0.170$) and spent 11.4 ± 6.4 and 17.7 ± 8.9 min hanging, respectively (nested ANOVA; $n = 136$; effect of reproductive

TABLE 1.—Results of tracking sessions conducted on 11 *Rhinophylla pumilio* (females F1–F9 and males M1–M2). Time budget parameters are given as means \pm SD per individual and part of night (1st part 1915 h to 2359 h and 2nd part 0000 h to 0615 h).

Individual	F1	F2	F3	F4	F5	F6	F7	F8	F9	M1	M2
Reproductive status ^a	NR	NR	NR	NR	L	L	L	L	SA	NR	NR
No. of tracking nights	5	3	5	5	5	5	5	4	5	3	4
Total contact time (%)	98.2	98.4	95.7	96.3	98	97.2	97.2	93.6	100	98.9	96.1
Spatial use											
No. of bearings	58	34	55	63	52	37	44	35	63	28	52
Home range (ha) (day roosts excluded)	12.3 (9.7)	5.8 (5.3)	16.9 (8.6)	9.2 (6.6)	10.7 (3.6)	4.5 (4.3)	5.9 (2.0)	7.5 (2.2)	5.8 (3.8)	9.0 (8.4)	2.5 (2.1)
Foraging area (95% kernel; ha) (no. foraging areas)	12.5 (1)	11.7 (1)	13.4 (1)	8.0 (1)	5.3 (2)	7.8 (1)	3.7 (1)	5.1 (1)	4.3 (1)	14.1 (1)	3.5 (1)
Core area (50% kernel; ha) (no. core areas)	2.4 (1)	0.6 (2)	1.6 (3)	1.2 (1)	0.7 (2)	0.7 (1)	0.5 (2)	0.6 (2)	0.2 (1)	2.1 (1)	0.5 (1)
Mean flight distances (m)	94 \pm 71	91 \pm 75	115 \pm 111	96 \pm 53	75 \pm 67	85 \pm 61	97 \pm 55	41 \pm 28	70 \pm 55	118 \pm 78	71 \pm 42
Hanging location revisitation (%)	15 \pm 9	27 \pm 1	19 \pm 12	13 \pm 15	29 \pm 19	24 \pm 13	20 \pm 14	41 \pm 8	25 \pm 15	0	14 \pm 12
Day roosts											
No. distinct day roosts	2	1	5	2	5	2	3	2	1	2	2
No. roosts out of foraging areas	2	1	1	1	3	0	3	1	1	2	0
Range of distances to the nearest foraging area (m)	75–130	5	280	150	165–365	—	100–430	475	120	25–35	—
Time budget											
Mean flight duration (min \pm SD)											
First part of night	9 \pm 5	8 \pm 5	9 \pm 4	12 \pm 7	10 \pm 6	15 \pm 6	14 \pm 8	13 \pm 5	5 \pm 2	12 \pm 5	7 \pm 5
Second part of night	11 \pm 6	11 \pm 4	11 \pm 5	13 \pm 6	11 \pm 5	13 \pm 6	17 \pm 7	14 \pm 7	9 \pm 6		
Mean cumulative flight time (min \pm SD)											
First part of night	104 \pm 25	89 \pm 7	110 \pm 22	121 \pm 23	79 \pm 29	106 \pm 16	128 \pm 18	117 \pm 7	60 \pm 9	110 \pm 16	79 \pm 29
All night long	196 \pm 38	160 \pm 17	213 \pm 51	255 \pm 50	199 \pm 42	234 \pm 34	316 \pm 37	252 \pm 31	135 \pm 31		
Mean duration of hanging phases (min \pm SD)											
First part of night	15 \pm 17	15 \pm 09	15 \pm 10	16 \pm 11	25 \pm 16	22 \pm 13	16 \pm 13	19 \pm 06	21 \pm 16	18 \pm 15	17 \pm 20
Second part of night	35 \pm 24	50 \pm 33	30 \pm 28	21 \pm 17	22 \pm 17	27 \pm 13	17 \pm 8	21 \pm 14	37 \pm 27		
Mean no. hanging phases per hour											
First part of night	2.28	1.58	2.80	1.94	1.56	1.44	1.73	1.80	2.20	1.76	2.27
Second part of night	1.25	0.76	1.68	1.63	1.76	1.44	1.66	1.32	1.28		

^a NR = nonreproductive; L = lactating; SA = nonreproductive subadult.

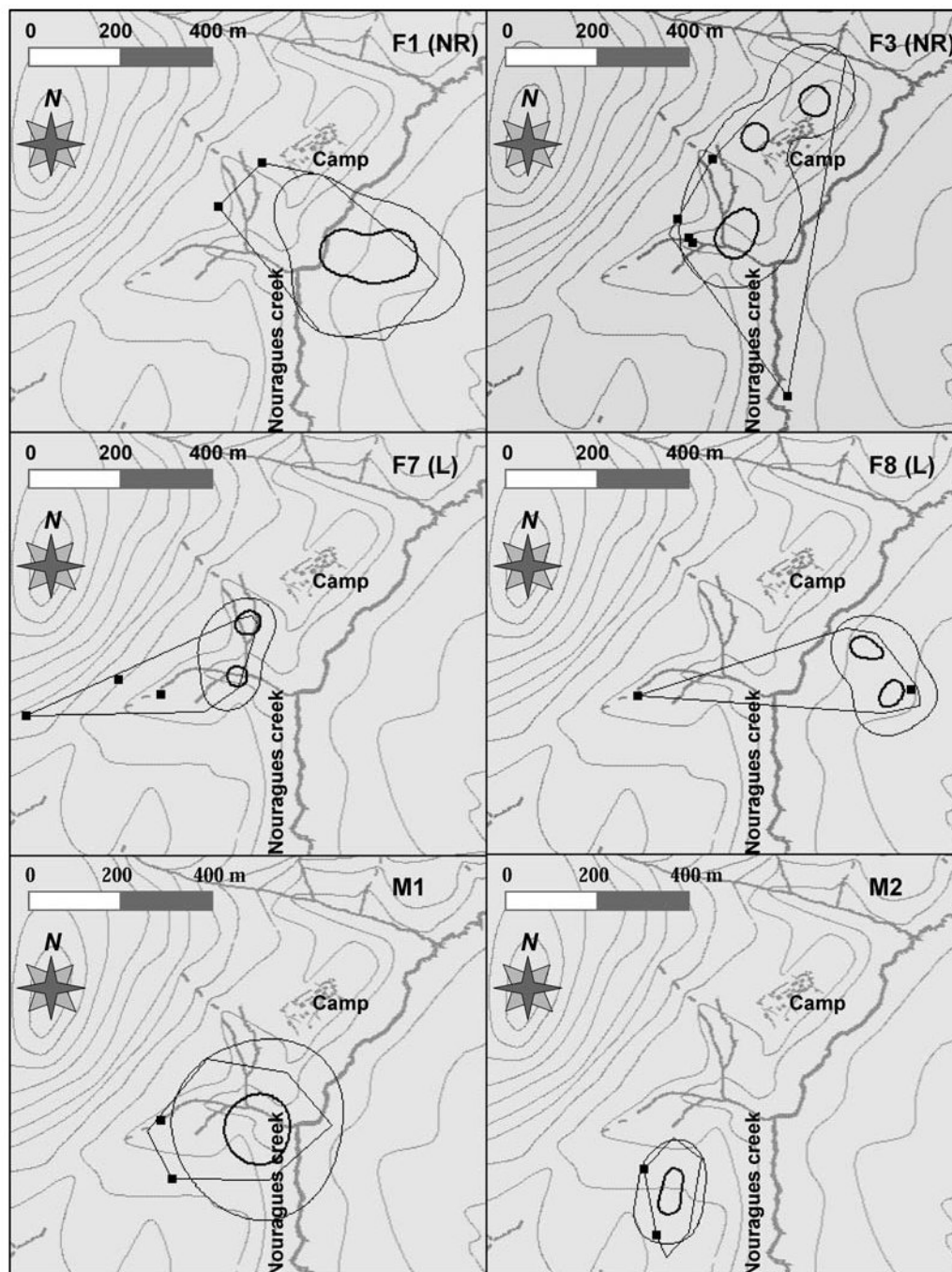


FIG. 1.—Examples of spatial use by 6 individual *Rhinophylla pumilio* at the Nouragues study area, including home range (100% inclusion convex polygon), foraging area (95% kernel, thin line), core area (50% kernel, bold line), and day roosts (black squares). Individual number and reproductive status (NR = nonreproductive females; L = lactating females) are indicated in upper right corners. Variation in height between isoclines (gray curves) is 20 m.

status: $F = 16.94$, $df. = 1$, 131, $P < 0.001$; effect of individuals: $F = 1.37$, $df. = 6$, 128, $P > 0.05$; $R^2 = 0.18$).

DISCUSSION

Movement patterns of R. pumilio.—The foraging strategy of *R. pumilio* as depicted by radiotracking fits our predictions based on the spatiotemporal distribution of its food. Given the

steady-state production of infructescences and the scattered distribution of epiphytes, we expected individual bats to spend most of their flight time in search flights, to use few and small foraging areas, and to conduct fewer and shorter commuting flights than fig-eating *A. jamaicensis*. As predicted, *R. pumilio* used a single foraging area and did not perform regular commuting flights while foraging. Female *C. castanea*, another medium-sized to small shrub-frugivorous bat, also tended to

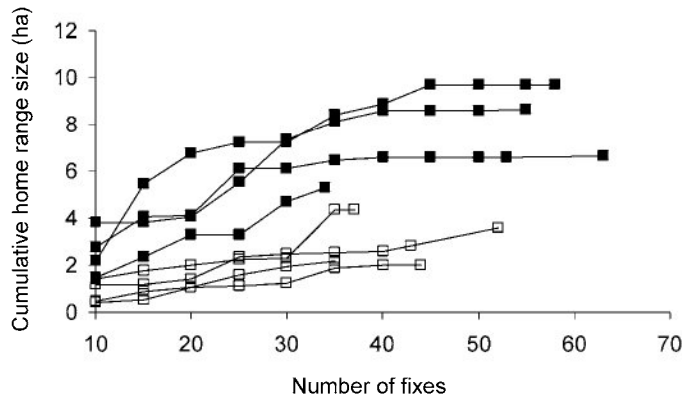


FIG. 2.—Cumulative values of home-range size (100% convex polygon, day roosts excluded) with increasing number of fixes for 4 nonreproductive and 4 lactating female *Rhinophylla pumilio* (closed and open symbols, respectively), showing that a plateau was reached in most cases.

use a single small foraging area (2.6–8.6 ha) like *R. pumilio*, but males foraged in up to 3 foraging areas (Thies 1998). Because only 2 males were tracked, we cannot rigorously compare the data sets.

Rhinophylla pumilio probably has the smallest home range ($\bar{X} = 8.2$ ha, range 2.5–16.9 ha) so far among the few frugivorous phyllostomid bats that have been studied to date. Although differences in methodological approaches preclude meaningful comparisons, both *C. perspicillata* and *A. jamaicensis* undoubtedly have larger home ranges. In Costa Rica, female *C. perspicillata* regularly commuted between and among day roosts and foraging areas at about 1–2 km (Heithaus and Fleming 1978). This represents 2–5 times the maximum flight distance we measured for *R. pumilio*. Distances were even greater for *A. jamaicensis*, which fed up to 10 km from its day roost in Mexico (Morrison 1978b). Only females of the shrub-frugivorous *C. castanea* had home ranges in Panama that were similar in size to those of *R. pumilio* ($\bar{X} = 13.7$ ha, range 5.5–34.9 ha—Thies 1998), whereas those of male *C. castanea* were 3 times larger.

However, small body size per se cannot explain the small home range of *R. pumilio*. Discrepancies in home-range size remained marked when comparing *R. pumilio* to other phyllostomid bats of similar size but different feeding modes. In particular, the small (9-g), trawling insectivorous *Macrophyllum macrophyllum* (Meyer et al. 2005) and the small (12-g), insectivorous *Lamproncycteris brachyotis* (Weinbeer and Kalko 2004), both radiotracked in Panama, displayed mean home-range sizes of 43 and 46 ha, respectively, reaching up to >150 ha in both species and even more for *L. brachyotis* if its distant day roost was taken into account. The medium-sized (25-g), gleaning, insectivorous *Lophostoma silvicolum* has an intermediate home-range size that still remains on average larger than those reported here for *R. pumilio* ($\bar{X} = 17$ ha, range 11–31 ha—Kalko et al. 1999; E. K. V. Kalko in litt.).

The small home-range size of *R. pumilio* compared to shrub-frugivorous bats may partly result from a greater proximity of

TABLE 2.—Results of nested ANOVAs regarding factors shaping nocturnal activity pattern of 4 nonreproductive and 4 lactating female *Rhinophylla pumilio*. The analyses evaluate the effects of reproductive status (nonreproductive versus lactating), interindividual variability, and part of night (1st part 1915 h to 2359 h versus 2nd part 0000 h to 0615 h). Probability values (*P*) are indicated in bold for significant effects.

Dependent variable and factors	<i>df.</i>	<i>F</i>	<i>P</i>
Flight distances (1st part of night)	(<i>n</i> = 318, <i>R</i> ² = 0.076)		
Reproduction	1, 310	8.957	0.003
Individuals (reproductive active)	6, 310	2.840	0.010
Hanging location revisitation rate	(<i>n</i> = 37, <i>R</i> ² = 0.325)		
Reproduction	1, 29	5.237	0.030
Individuals (reproductive active)	6, 29	1.393	0.251
Cumulative flight duration (1st part of night)	(<i>n</i> = 37, <i>R</i> ² = 0.407)		
Reproduction	1, 29	0.060	0.808
Individuals (reproductive active)	6, 29	3.319	0.013
Cumulative flight duration (all night long)	(<i>n</i> = 37, <i>R</i> ² = 0.617)		
Reproduction	1, 29	11.331	0.002
Individuals (reproductive active)	6, 29	6.066	0.001
Duration of flights	(<i>n</i> = 648, <i>R</i> ² = 0.100)		
Reproduction	1, 638	26.980	0.001
Part of night	1, 638	6.391	0.012
Reproduction × part of night	1, 638	1.445	0.230
Individuals (reproductive active)	6, 638	5.244	0.001
Duration of hanging phases	(<i>n</i> = 665, <i>R</i> ² = 0.118)		
Reproduction	1, 655	0.355	0.552
Part of night	1, 655	35.756	0.001
Reproduction × part of night	1, 655	24.833	0.001
Individuals (reproductive active)	6, 655	4.682	0.001
No. hanging phases/h	(<i>n</i> = 74, <i>R</i> ² = 0.553)		
Reproduction	1, 64	3.881	0.053
Part of night	1, 64	39.244	0.001
Reproduction × part of night	1, 64	29.060	0.001
Individuals (reproductive active)	6, 64	1.247	0.295

day roosts to foraging areas (<475 m for *R. pumilio*, versus 1.2–1.6 km for *C. castanea* and *C. perspicillata*, respectively—Heithaus and Fleming 1978; Thies 1998). These differences in distance are likely to be associated with different roosting behaviors between the “nomadic” *R. pumilio* on one hand, which forms small groups and regularly shifts day roosts, and the *Carollia* species on the other hand, considered as refuging species (sensu Hamilton and Watt 1970) that form larger colonies in more permanent day roosts to which they are rather faithful (Heithaus and Fleming 1978; Thies 1998). Lower roost fidelity is probably associated with higher roost availability (Lewis 1995). Accordingly, as many as 35% of identified day roosts used by *R. pumilio* in our study were actually unmodified leaves of juvenile palms ranking among the dominant species of the local palm community (de Granville 2001), suggesting a high availability of potential roosting sites compared to caves and hollow trees used by *Carollia* species.

We found evidence that individual *R. pumilio* regularly roosted outside the immediate vicinity of their respective foraging areas, probably to interact with conspecifics. We propose that 2 advantages of roosting in a group for *R. pumilio*

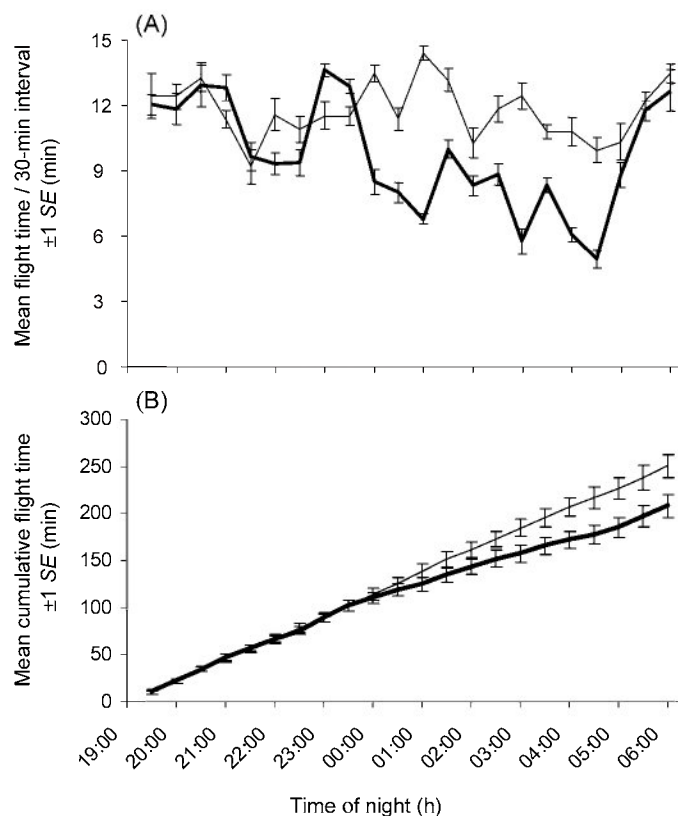


FIG. 3.—A) Mean flight time per 30-min interval and B) mean cumulative flight time between 1915 h and 0615 h for 4 non-reproductive (bold line) and 4 lactating female *Rhinophylla pumilio* (thin line).

are predator avoidance and thermoregulatory advantages. More individuals increase the mean vigilance level of the group and thus the chances of detecting predators. Furthermore, hanging in a cluster contributes to reducing heat losses (Kurta 1985; Tuttle 1976). The latter point may be crucial because temperature in tents used by *R. pumilio* is not buffered against fluctuations and also not warmer than ambient temperature. Yet, even in tropical lowland forests, ambient temperatures at understory level (23–29°C) is below the thermoneutral zone of small bats during most of the daytime (31–32°C for <15-g species—Speakman and Thomas 2003). The formation of clusters may help compensate for low ambient temperatures.

Evidence for an increase in food intake by lactating females.—We expected the physiological constraints of lactation to force females to substantially modify movement patterns. As a proximal constraint of lactating, female bats need to increase their food intake for producing milk (Anthony and Kunz 1977; McLean and Speakman 1999) as in other small mammals (e.g., Rogowitz and McClure 1995). Food intake can be roughly quantified by the number of flights per unit of time as has been done for *C. perspicillata*, which carries and consumes food items in temporary night roosts (Charles-Dominique 1991). In our study, the number of flights and hanging phases per night remained unchanged among reproductive groups, suggesting that lactating *R. pumilio* did not

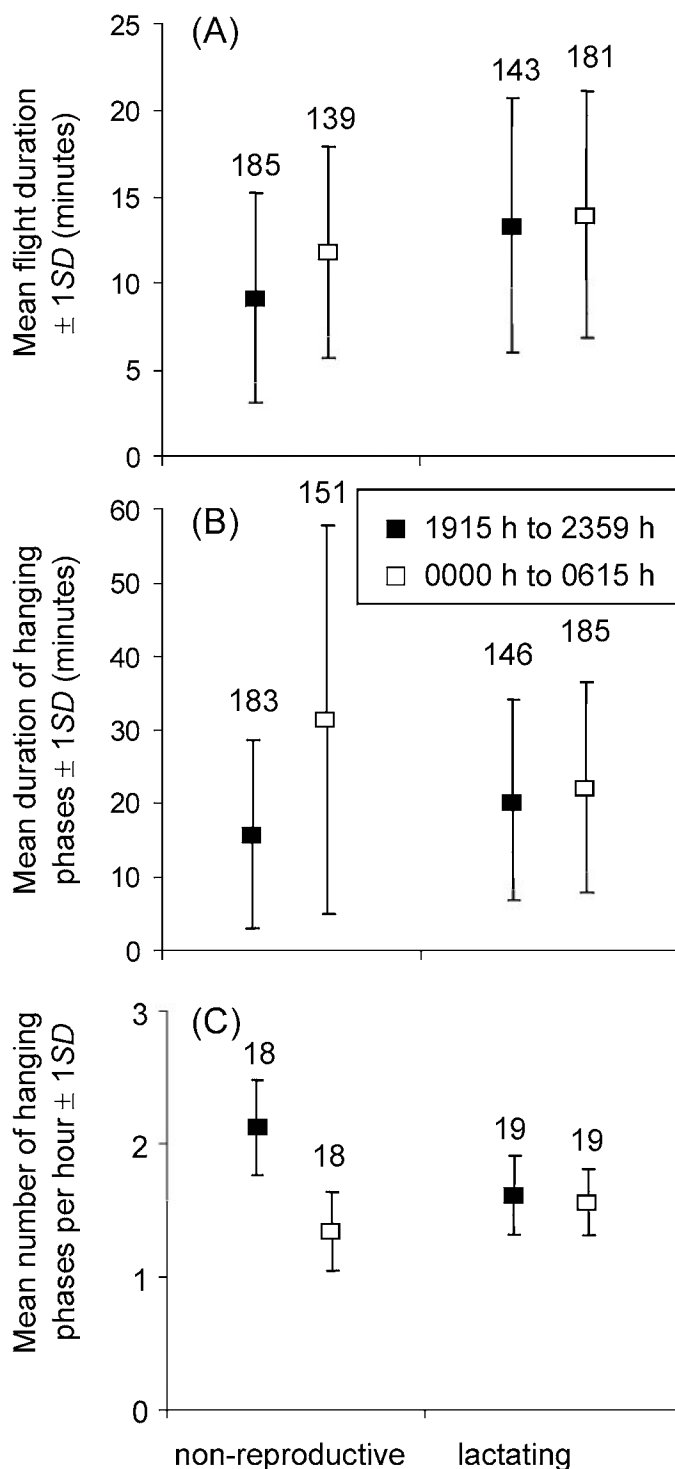


FIG. 4.—Time activity budget of 4 nonreproductive and 4 lactating female *Rhinophylla pumilio* during the 1st and 2nd part of night, including A) mean duration of flights, B) mean duration of hanging phases, and C) mean number of hanging phases per hour. Sample sizes are indicated above bars (see Table 2 for statistics).

visit more epiphyte infructescences than did nonreproductive ones. However, the durations of the hanging phases by lactating females during peak foraging activity after dusk exceeded those of nonreproductive females by about 55%.

Thus, increased food intake is probably achieved through increased duration of visits to epiphytes with ripe fruits.

The hypothesis that lactating female *R. pumilio* increase their food intake by ingesting more pulp per visit to individual epiphyte infructescences might hold true if they display a greater gut capacity or a faster food intake or assimilation process than nonreproductive females. Milk production combined with the suckling of the young requires mobilization of both water and nutrients at mammary glands (e.g., Kunz and Hood 2000; Kurta et al. 1989, 1990), and thus may allow faster food processing by expelling ingested water at a greater rate, which in turn may allow lactating *R. pumilio* to ingest more pulp at each hanging phase. Alternatively, by extending the mean duration of hanging phases beyond 15–20 min, lactating bats may have time to cover most of the 1st digestive cycle, partly emptying their gut after a rapid passage of food through the digestive tract (5–30 min for *R. pumilio*—Cockle 1997), and initiating a 2nd feeding cycle on the same infructescence. Infrared video recordings of bats foraging on ripe infructescences are required to test these hypotheses.

Effect of reproductive status on movement pattern.—Compared to nonreproductive females, lactating female *R. pumilio* did not use smaller home ranges. Furthermore, they did not select day roosts closer to their respective foraging area nor did they display higher site fidelity to day roosts. On the contrary, they often roosted well outside of their foraging area, which means that nocturnal nursing obligates them to either regularly commute back to their day roost at nighttime or to transport their young into their foraging area. We found indirect evidence that females transport their young to temporary night roosts in their foraging area at night and regularly fly back to feed it. This scenario stems from the observations that lactating females did not leave their young in the day roosts during the night, never returned to day roosts situated outside of their foraging areas during the night, and revisited significantly more often (+56% according to our estimations) hanging locations that they had already visited earlier in the night compared to nonreproductive females. Accordingly, lactating *R. pumilio* mistnetted at the beginning of the night were more likely to carry a young than lactating females caught later at night (J.-F. Cosson and M. Delaval, pers. comm.).

This result is similar to observations on other fruit bats (*C. perspicillata* and *Uroderma bilobatum*—Cosson 1994; Lewis 1992) and nectar bats (e.g., Baumgarten and Vieira 1994) that also are known to transport their young. Transportation of young from the day roost to different night roosts may reduce predation pressure at day roosts during nighttime, and it also may be necessary if the young eat fruits with their mother before they become volant (Fenton 1969). In contrast to our observations, insectivorous female bats that form maternity colonies leave their young in the day roost while foraging, and then regularly come back for nursing during the night (e.g., Grinevitch et al. 1995; Henry et al. 2002; Swift 1980).

Although transporting young into their foraging area imposes additional energy expenditure on females, it also may allow substantial energy saving because they do not need

to regularly commute back to their day roost for nursing. This may allow females more foraging time. Indeed, modifications of movement patterns accompanying lactation in this study suggest that breeding females may be under time pressure when foraging. On one hand, they maintained high flight activity all night long and on the other hand, they reduced the size of their foraging area and flight distances by 42% and 25%, respectively, compared to nonreproductive females. Temperate insectivorous bats also tend to forage longer when lactating (up to >100%—Barclay 1989; Rydell 1993) and to reduce their home range by up to 51% (Henry et al. 2002; Racey and Swift 1985; Swift 1980). In these species, births are generally synchronized with peak insect abundance in summer, making it impossible to distinguish between the respective effects of lactation and food availability on activity rhythm (Henry et al. 2002).

Reducing the spatial range of activity could be considered a mechanism of energy compensation during lactation, providing it allows females to decrease flight duration (e.g., by 35% for *C. perspicillata*—Charles-Dominique 1991) and hence to reduce energy expenditure. However, in the case of lactating *R. pumilio*, this statement is partly discredited by the 18–46% increase in flight durations. Tentatively, we propose that lactating females may spend more time in search flight to locate food sources as close as possible to temporary night roosts where they left their young, and that their flight maneuverability and speed are altered because of the ingestion of greater quantities of pulp on epiphyte infructescences.

Overall, we cannot fully exclude the possibility that part of the observed differences in movement patterns also is influenced by the small sample size of our study with only 8 individuals. Interindividual variations observed for 5 of the 7 study parameters were high (Table 2). Expanding the tracking data sets to permit comparison of movement patterns among 2 or more categories of individuals (e.g., males versus females or reproductive versus nonreproductive females) based on number of individuals as the unit of analysis rather than duration of sampling session for each individual should be prioritized. Likewise, controlling for possible confounding effects related to seasonality, resource phenology, or other environmental factors may further reduce inter-individual variations.

*Sensitivity of *R. pumilio* to forest fragmentation.*—As outlined by our study, search flights are an important component of the foraging strategy of frugivorous bats feeding on a spatially scattered food resource. This foraging strategy would be less efficient within fragmented forest remnants embedded in a matrix devoid of fruiting plants. This is particularly true for *R. pumilio*, which is specialized to forage on epiphytes of forest understory that do not establish well in dry, secondary growth areas (Cockle 1997, 2001). Eventually, small shrub-frugivore bats may not be able to efficiently exploit a highly fragmented habitat in which they are forced to repeatedly conduct long commuting flights. As an alternative but not mutually exclusive explanation, small shrub-frugivore bats may not be able to afford long commuting distances between fragments in contrast to larger fruit-eating bats. Larger bats conduct faster and longer flights because of higher wing

loading, which is energetically beneficial for commuting (Norberg and Rayner 1987). Conversely, smaller bats fly less efficiently than larger bats (Speakman and Thomas 2003) because a greater proportion of energy expenditure during flight is lost as heat dissipation (96% versus 75–80%).

Assessing whether foraging strategy, body size, or both are crucial with regard to tolerance of fragmentation requires more tracking studies of *R. pumilio* in forest fragments of various sizes and degree of isolation. For instance, a tracking study on *Artibeus watsoni*, another small frugivore that frequently feeds on figs, revealed regular commutes over expanses of inhospitable matrix (water) in search of fruits in the canopy (L. Albrecht et al., in litt.).

We believe that constraints imposed by rearing young represent a particularly critical factor for female *R. pumilio* in fragmented habitats as well as for females of other small bat species whose foraging strategy consists largely of search flights. Lactating females cover shorter distances and spend more time foraging, while forest fragmentation imposes longer flight distances because animals have to fly back and forth between fragments. This adds up to a cumulative time and energy loss. Although some studies report evidences of breeding activity in fragmented habitats (Estrada and Coates-Estrada 2002; Henry 2005), this does not necessarily indicate that breeding success equals that of populations established in continuous forest. Further studies are needed to test the prediction that females in fragmented forests experience severe fitness reduction, reflected in population dynamics or parameters of physiological stress such as stress hormone measurements.

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