Chapter 14
The Influence of Sex and Reproductive Status on Foraging Behavior and Seed Dispersal by *Uroderma convexum* (Chiroptera: Phyllostomidae)

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Abstract *Uroderma convexum* construct and occupy tents. Tents serve as day shelters and reproductive sites, but also frequently are used as night feeding roosts. We observed and radio-tagged *U. convexum* occupying tents at Sarapiquí, Costa Rica. Social groups of *U. convexum* were composed of one adult male, reproductive females, and immature bats apparently forming a polygynous harem organization. We report spatial information (core-use, foraging range, habitat coverage use) and seed dispersal behavior for seven radio-tagged bats. Bats spend much of their foraging time in the riparian habitats; however, they also forage in mature and secondary forest and several anthropogenic habitats, dispersing at least eleven species

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of plants of different life forms. Bats establish night feeding roosts up to 1800 m from their day roost. Feeding roosts are in foliage close to plants producing ripe fruits and both feeding roosts and resource plants vary in space over time. Most of the time, adult males restrict movements to fruiting plants within 100 m of their tents and frequently return within the foraging period of the night, thus males disperse a large proportion of the seeds they handle exclusively within perturbed areas associated with the tents. In contrast to males, adult females usually do not return to a tent until near dawn and move over greater distances, frequently dispersing seeds into multiple habitats. Social organization, sex, and reproductive status appear to influence the outcomes of foraging behavior and seed dispersal of the bats.

14.1 Introduction

Many animals are noted for constructing shelters that offer protection from weather and predators, as well as places to rear offspring. These include numerous mammals that excavate burrows (e.g., rodents, moles, aardvarks, armadillos, carnivores, among others). Notable examples are the woodrats (*Neotoma* spp), round-tailed water rats (*Neofiber alleni*), muskrats (*Ondontra zibethica*), and beavers (*Castor fiber* and *C. canadensis*) for their behavior of introduction and inter-weave plant materials into house-like shelters above ground or under water. However, among more than 1300 recognized species of bats (N. Simmons *personal communication*), only a few invest time and energy to modify their environment for the purpose of creating a roost. *Lophostoma silvicolum* males are unique in carving holes with their teeth to modify termite nests which often continue to have living termites that actively aerate the nests (Dechmann et al. 2004); however, 22 species of bats are known to modify living plant parts, mostly leaves, in order to build "tents" for group shelters (Rodríguez-Herrera et al. 2007). Tent-making has evolved in the Pteropodidae in the genus *Cynopterus* which occurs in southern Asia and some Indo-Pacific Islands and in nine genera of the Phyllostomidae of the Neotropics.

Tent-making bats are social, they form groups. Group size in tents varies between seasons and species. The causes of sociality in tent-making bats remain unclear. Kerth (2008) suggests that ecological constraints such roost limitation, social thermoregulation, and longevity may promote sociality, but these constraints are not sufficient to explain the current frequency and diversity of group living in bats. Furthermore, it has been suggested that polygyny in tent-making bat species is based on the defense of the tent resource (Balasingh et al. 1995; Brooke 1990; Chaverri and Kunz 2006; Kunz and Lumsden 2003; Kunz and McCracken 1996; Kunz et al. 1994; Storz et al. 2001). The generally assumed hypothesis is that males make the tents and females select a male based on tent characteristics. Tent construction is also assumed to be a proxy for male display behavior in competition with other males for females (Balasingh et al. 1995; Kunz and Lumsden 2003; Kunz and McCracken 1996). Nevertheless, this hypothesis has never been tested and the little evidence available suggests that this assumption may vary according

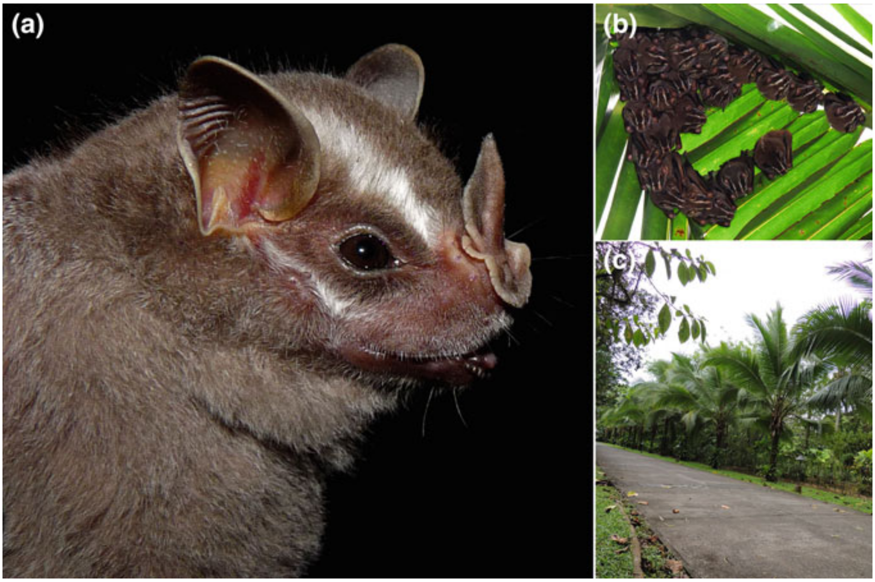


Fig. 14.1 **a** *Uroderma convexum*; **b** group of *U. convexum* in a pinnate tent, **c** coconut palms with tents of *U. convexum*

to species. For example, at least for the Honduran white bat, *Ectophylla alba*, not only the males construct their tents, females also contribute to this task (Rodríguez-Herrera et al. 2006, 2011). Unfortunately, the process of tent construction by Neotropical tent-making species had never been directly observed for most of the species, and until this information become available, assumptions have to be done regarding social life and implication of sex differentiation on the behavior of bats (e.g., foraging behavior) around their roosting resource.

Although tents are clearly important for day roosting, in this chapter, we focus primarily on the importance of this kind of roosts as central places for the nightly origin point for foraging movements in the phyllostomid *Uroderma convexum* (Fig. 14.1a). We discuss our findings in the context of the hypothesis proposed by Kunz and McCracken (1996) that adult males actively construct and defend tents in order to attract harems of breeding females while presenting spatial information on the size of foraging ranges and habitat use by adult males and adult females. We then present information on seed dispersal examining the relationships between tent locations, foraging areas, and the handling time associated with ingestion of fruits.

We tested the following predictions: (1) Given their tent defense behavior, nightly activity of adult males will be restricted to areas near roosting resources, which results in small movement areas; (2) Adult females will show less restricted movements during nightly activities, which results in larger movement areas than adult males; (3) If adult males do not restricted their movements close to tents, they probably will return frequently to their roosts during the night (monitoring pattern);

(4) Due to the reason that they are not constrained by tent defense, adult females may disperse seeds over greater distances and in more habitats than males.

14.1.1 Taxonomical, Behavioral, and Ecological Profile of Uroderma convexum

Mantilla-Meluck (2014) recognized five species of Uroderma throughout its geographic range (*bilobatum*, *convexum*, *davisi*, *magnirostrum*, and *bakeri* sp. nov.). Based on this work, *U. convexum* (Lyon 1902) is recognized as occurring from Ecuador, Colombia, and the Pacific coast of Panama west to Honduras and the Atlantic versant of Mexico. In Costa Rica, *U. convexum* typically inhabit lowlands of the Pacific and Caribbean coast, below 1200 m elevation (LaVal and Rodríguez-Herrera 2002; Rodríguez-Herrera and Wilson 1999). The diet of this genus is composed primarily of fruit with lesser amounts of pollen, nectar, and insects associated with fruits or flowers (Fleming et al. 1972; Gardner 1977; Handley et al. 1991). Uroderma as a genus consumes fruits of approximately 40 known plant species from 13 genera and 10 families (Lobova et al. 2009). *Ficus* species are prominent in the diet which also includes the genera *Piper*, *Philodendron*, *Cecropia*, *Solanum*, *Vismia*, *Quararibea*, *Clusia, Brosimum*, and *Psidium* (Gianini and Kalko 2004; Goodwin and Greenhall 1961; Lovoba et al. 2009). Its generalist frugivorous diet, habitat breadth, and abundance suggest that all five species of the genus are important seed dispersers of both small and large-seeded fruits promoting plant community diversity and secondary succession in open areas and forest fragments (Fleming 1988; Fleming and Heithaus 1981; Gorchov et al. 1993).

Uroderma roost by day under tents made from modified leaves of 18 identified species of plants (Figs. 14.1b and 14.2a, b; Barbour 1932; Kunz 1982; Rodríguez-Herrera et al. 2007). In many locations they prefer the pinnate leaves of *Cocos nucifera* for tent construction (Figs. 14.1b and 14.2a; Sagot et al. 2013;

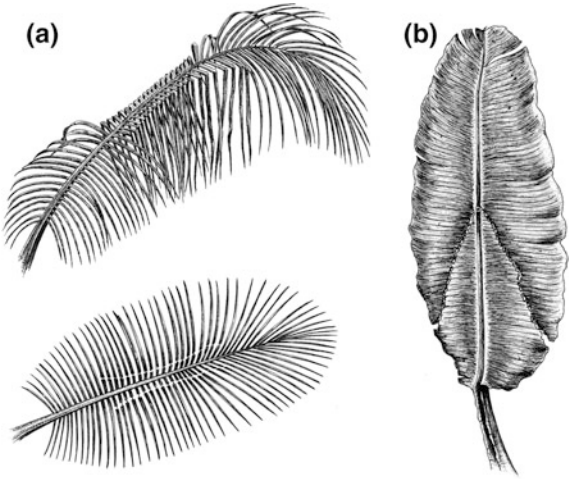


Fig. 14.2 Architecture of the tent roosts used by *U. convexum* at the study site. **a** Pinnate tents in *C. nucifera*; **b** paradox tent in *Musa* spp. Modified from Rodríguez-Herrera et al. (2007)

Timm and Lewis 1991). Occasionally, *U. convexum* roost in hollow logs, caves, unmodified leaves, and human buildings (Lewis 1992; Timm and Lewis 1991). The use of *C. nucifera* and other introduced plants have favored the presence of *U. convexum* tent roosts in anthropomorphic habitats such as plantations, gardens, and cattle ranches; however, this species also inhabits mature forest of various types (Bonaccorso 1979; Sagot et al. 2013).

Uroderma is gregarious (Fig. 14.1b), although usually found in groups of <15, it has been observed forming colonies with up to 59 individuals (Kunz 1982). Reproduction is a bimodal polyestry with immature flighted and independently foraging at about one month of age (Fleming et al. 1972). Social groups are composed of multiple females and dependent young with a single reproductive male present, suggesting a harem mating system (Baker and Clark 1987; Kunz and McCracken 1996).

14.2 Study Area

Our study was conducted between July 2012 and August 2013 at the Tirimbina Biological Reserve (TBR) and surrounding landholdings at La Virgen de Sarapiquí, Heredia Province, Costa Rica (Fig. 14.3). This area is tropical wet forest (Holdridge 1967) with elevation ranging from 40 to 150 m. Mean annual temperature is 25.3 °C and mean annual precipitation is 3900 mm (McDade et al. 1994). TBR includes primary, secondary, and riparian forest as well as a small abandoned cacao (*Theobroma cacao*) plantation. Surrounding landholdings form a matrix of anthropomorphic habitats including gardens, pastures, and diverse agricultural plantations.

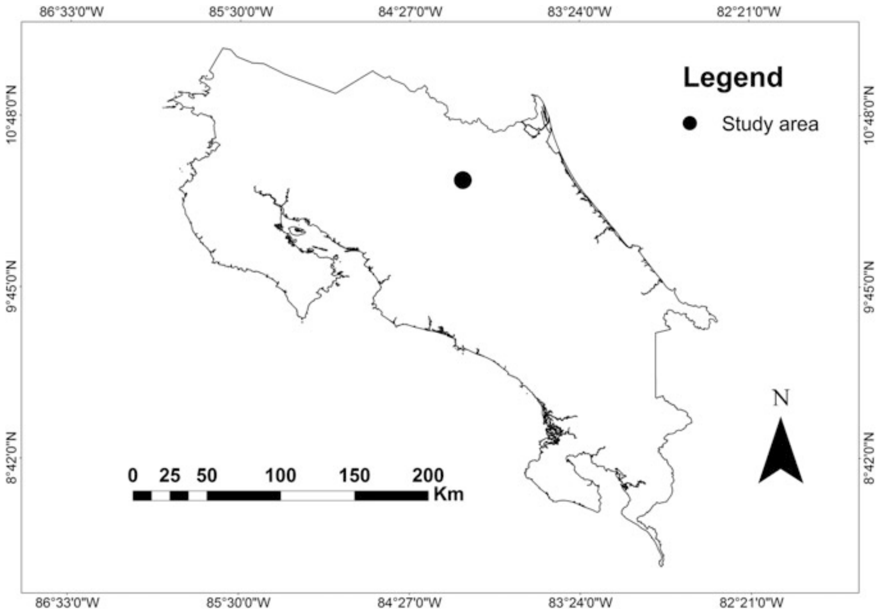


Fig. 14.3 Location of the study area. La Virgen de Sarapiquí, Heredia, Costa Rica

14.3 Methods

14.3.1 Capture of Bats

Our research protocols followed the guidelines of the American Society of Mammalogists (Sikes et al. 2011). Bats were captured under a series of modified pinnate tents made from coconut palm fronds and paradox tents made from banana leaves (Figs. 14.1c and 14.2b). Individual bats were captured during the day using a customized trap with an extendable pole designed to catch a group of bats within a tent. Bats also were captured at night using mist nets placed close to tents or fruiting trees. Upon capture bats were placed in soft cloth bags and taken to an enclosed area where they could be processed. Body mass and forearm length were measured using a 100 g Pesola spring balance (Baar, Switzerland) and CD-80C Mitutoyo digital calipers (Aurora, Illinois, USA), respectively. Individuals were classified as adult or immature based on the ossification of the epiphyseal growth plates of the phalanges (Anthony 1988). Reproductive status was determined from enlarged testes on males and pregnancy or lactation for females.

Captured bats were selected for two purposes: some were used for captive observations of fruit manipulation during feeding and others for radiotracking. Several individuals were used for both activities. Bats selected for radiotracking were fitted with a colored, split ring, plastic forearm band (Size X3, A. C. Hughes, Hampton Hill, United Kingdom) for long-term individual recognition and with a radio transmitter (model BD-2 N, Holohil Systems, Carp, Ontario, Canada). Transmitters were glued to the dorsal fur between the scapulae (Audet 1990; Bonaccorso et al. 2015; Waldien and Hayes 2001; Waters et al. 1999) using latex adhesive (Osto-Bond; Montreal Ostomy; Montreal, Canada). Transmitter mass was 0.5 g, < 3 % of body mass of the smallest bat that we radio-tracked. Bats were held in a soft cloth bag for 20 min to ensure that the adhesive securely bonded the transmitter to the fur. Bats were then released at the point of capture within 40 min of capture. Based on observations of tagged bat on their tents and recaptures of the animals, it appeared that transmitter's weight and plastic rings did not affect the bat's health or flight capacity.

14.3.2 Radiotracking

Bats were monitored during nightly tracking periods between 1730 and 0000 h. Multiple individuals were monitored in a given night using TRX-1000S tracking receivers and 3-element directional yagi antennas (Wildlife Materials, Murphysboro, Illinois, USA). Tracking stations were established within 10 m of tents and always <300 m from foraging areas for each bat. UTM coordinates of tracking stations, tents, night roosts, and fruiting trees were recorded using Garmin 12XL GPS units (Garmin Corporation, Olathe, Kansas). Azimuths from the tracking station to the bearing determined with the directional antenna were measured to the nearest degree using KB series sighted compasses (Suunto, Helsinki, Finland).

Observers frequently moved between tracking stations to improve radio signal strength and proximity to bat activity in order to reduce computational errors in determining bat positions. When radio contact with a focal animal was lost, we quickly re-established radio contact by walking in the direction of the disappearing radio signal. If two or more bats were within effective telemetry range, tracking data were taken every 3 min as possible rotating signal reception between multiple tagged bats. Flight and roosting were distinguished by a rapidly varying signal strength indicating flight and a steady signal at fixed directionality for at least 15 s indicating roosting (Bonaccorso et al. 2015; Rothenwöhrer et al. 2010). Each radio fix included records of time, signal strength from an analog meter, gain setting from gradations calibrated on the gain dial, the GPS position of the observer, and the activity of the bat (roosting or flying). Based on data inspection of the activity points and the capacity of bats of flying across the long axis of all measured foraging ranges in < 3 min, we concluded that all spatial points in our analyses were independent.

14.3.3 Calculation of Bat Locations

Telemetry locations for roosting bats were determined by homing (walking toward increased signal strength) to roosting bats or by triangulation using three or more positional fixes if roosts could not be approached because of physical barriers such as rivers or fences. Flight positions were determined from single azimuths along with distance, which was estimated from signal strength and gain following established methods of Bonaccorso et al. (2015), Law and Lean (1999), O'Donnell (2001) and Winkelmann et al. (2000). Approximate relationship of signal strength to distance (± 30 m error) was calibrated from transmitters set both at 2 and 15 m above ground at standardized gain settings along measured reception distances to 300 m. The majority of single bearing records were made with the observer <100 m from the transmitting bat while avoiding topographical features potentially causing severe refraction or reflection of radio signals.

Telemetry data at noted above including distance estimates between observer and bat were entered into Excel (Microsoft 2012). We used LOAS 4.0 (Ecological Software Solutions, Urnäsh, Switzerland) to plot triangulations of the estimated location of the bat; whereas, bat locations from single bearing telemetry were calculated using the following equations:

$$BN = (ON + D)\ \sin\Theta \tag{14.1}$$

$$BE = (OE + D)\ \sin\Theta \tag{14.2}$$

Where BN is the northing UTM location of the bat, ON is the northing UTM location of the observer, D is the estimated distance based on signal strength, Θ is the azimuth in radians from the observer to the bat, BE is the easting UTM location of the bat, and OE is the easting UTM location of the observer.

14.3.4 Landscape Spatial Analysis and Mapping

We employed a least squares cross validation to determine the smoothing parameter (Rodgers and Carr 1998) with minimum estimated error for fixed-kernel estimates (Seaman et al. 1999). From these data, we calculated minimum area probabilities for foraging range (FR) as the 95 % fixed kernels and Core-use Areas (CUA) as the 50 % fixed kernels. Kernel value calculations were obtained by Geospatial Modeling Environment (2009–12), ArcGIS (ESRI 2010) and (R Core Team 2013). Flight positions as well as night roosting positions were used to calculate FR and CUA. Long Axis across the foraging range (LAX) was determined by measuring the distance between the two farthest point locations within the FR. Finally, we calculated the percentage of activity of the bats within and beyond 100 m away from the day roosts (PAC).

To examine the use of the space by *U. convexum* and its potential relationship to seed dispersal, we transposed bat locations on a map of the study area using ArcGIS and classified the land cover as: (1) Forest: closed canopy upland forests; (2) Gardens: associated with horticulture; (3) Pasture: grasslands dedicated to cattle grazing; and (4) Riparian: bands of gallery forest along the Sarapiquí River and small streams. We tallied the number of telemetry positions for each bat that fell into each habitat category to obtain the percentage of use per habitat.

14.3.5 Seed Dispersal

In addition to the use of tents by *U. convexum* as day shelters (Barbour 1932; Kunz 1982; Rodríguez-Herrera et al. 2007), tents also are used for feeding at night (Rodríguez-Herrera et al. 2007). We noted the number and species of seeds discarded under tents by *U. convexum* following the sampling methods used by Melo et al. (2009). We searched for and sampled pinnate tents in *C. nucifera*, due to the high density of these tents in gardens and along roads of Sarapiquí (Sagot et al. 2013). Tents with *Uroderma* are occasionally found in closed canopy forest; however, because other bat species may use these tents in this habitat, we excluded such tents from our seed analysis (Rodríguez-Herrera et al. 2007). Pinnate tents of *C. nucifera* in the study area were scanned for seeds on the soil surface in 1 m^2 quadrats immediately beneath tents. We also collected seeds in control quadrats established in each of the four cardinal directions 5 m away from each tent. We differentiated between bat-generated and non-bat seed rain by characteristic tooth and claw marks of the bats. All seed collection was restricted to seeds >8 mm length (large seeds) because smaller seeds are difficult to identify and may be carried away by water run-off or ants (Melo et al. 2009). Buried seeds were excluded to avoid older seed rain that may have occurred before tent construction. We excluded those seed species found in similar densities in both tent and control quadrats. Seeds collected were identified to the finest taxonomic level and classified according to associated habitat (Table 14.3). We also examined the diets of our radio-tagged bats based upon visual inspection of fruiting trees having ripe fruit crops in areas frequently visited by tagged bats or from fruits found under feeding roosts.

14.3.6 Captive Observations of Fruit Manipulation by U. convexum

We employed a screened tent to observe fruit manipulation and consumption by bats. We offered one male and one female in each trial fresh ripe fruits, either *Ficus insipida* or *F. citrifolia,* obtained each day from fruiting trees in the area. Fruit height and width were measured with CD-80C Mitutoyo digital calipers (Aurora, Illinois, USA), weighed with a ACP-200 Digital pocket scale (American Weigh Scales—Georgia, USA), and numerically marked with ink. Fruits were offered to the bats attached by paper clips onto a horizontal rope 2 m above the ground. For each feeding attempt, we noted the identity of the bat, time taken consuming the fruit and the fruit mass consumed (difference between the initial wet mass of the entire fruit and the mass of discarded fragments). We used a Sony DCR-SR45 digital video camera recorder with night vision (Sony, New York, USA) to recorded and analyzed fruit consumption behavior. We only included in our analysis for fruit handling time fruits that were entirely consumed.

14.3.7 Statistical Analysis

We compared FR, CUA, PAC, and habitat use among sexes using one-way ANOVAs with an a posteriori test of Tukey's Honest Significant Difference (Tukey HSD). Also, 2-way ANOVAs were performed to compare fruit consumption time and initial fruit wet mass among sexes. For the analyses of PAC, processing time of fruits of *F. citrifolia* and habitat use (from gardens only), we employed a logarithmical transformation to fit the parametric analyses. We used a Kruskal–Wallis rank sum test for comparison of LAX between sexes. Although we radio-tagged and tracked 10 bats, we excluded from our spatial analyses of FR, CUA, and LAX all immature bats and individuals that had ≤100 total telemetry location points. All numerical results reported in the text are means and standard errors. All analyses were conducted using (R Core Team 2013) with an alpha level of ≤0.05.

14.4 Results

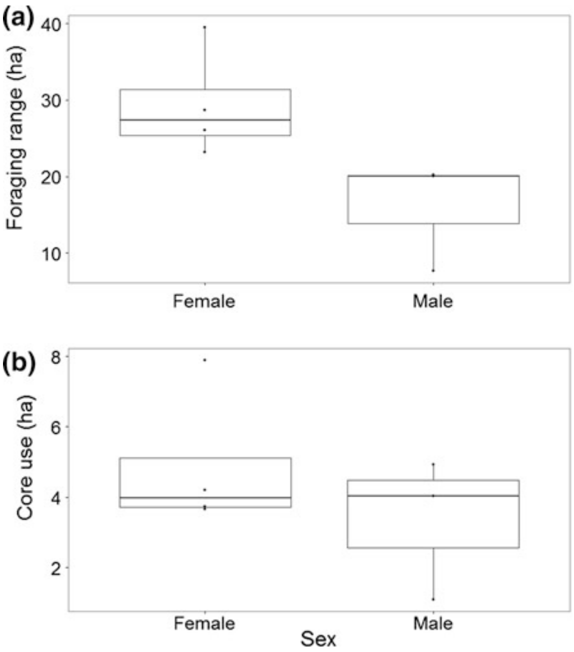
Seven *U. convexum,* represented by three adult males and four adult females were radio-tracked for two to ten calendar days (4.71 ± 1.06 days/bat). We collected a total of 1236 telemetry locations for these seven individuals (Table 14.1). Sub-adult

Table 14.1 FR, CUA, and LAX of *U. convexum* at Sarapiquí

Sex/ind.	Month/year	Tracking nights	Telemetry positions	95 % FR	50 % CUA	LAX	Activity ≤100 m from tent
		(n)	(n)	(ha)	(ha)	(m)	(%)
M2	Jul-12	10	423	7.7	1.1	1817	94.5
M3	Aug-13	2	103	20.1	4.9	583	26.2
M4	Aug-13	3	111	20.2	4.0	601	18.0
F3	Jul-12	7	144	23.2	3.7	872	8.3
F4	Aug-13	3	160	28.7	4.2	848	3.1
F5	Aug-13	4	170	39.5	7.9	1135	8.8
F6	Aug-13	4	125	26.1	3.7	783	17.6
Mean ± SE		4.71 ± 1.06	176.57 ± 42.11	23.63 ± 3.66	4.21 ± 0.76	948 ± 160.9	25.21 ± 11.90

M Adult male; *F* Adult female

Fig. 14.4 Median (quartiles and range) of the FR (**a**) and CUA (**b**) of male and female *U. convexum* at Sarapiquí



male M1 and adult females F1 and F2 were excluded from our analysis of FR, CUA, LAX, PAC, and habitat use because of small sample sizes <50.

Mean FR for *U. convexum* was 23.6 ± 3.6 ha (*n* = 7 bats; Table 14.1). Although a one-way ANOVA slightly missed significant difference between female and male FR (Tukey HSD test, *P* = 0.06) in part due to high variance, females trended toward higher median values of FR than males (Figs. 14.4a and 14.5a).

Mean CUA was 4.21 ± 0.76 ha (*n* = 7 bats; Table 14.1). There were no significant differences between sexes in CUA (TukeyHSD test, *P* = 0.37). Females and males had similar CUA medians; however, again there was high variation in individual values for both sexes (Figs. 14.4b and 14.5b).

Mean LAX was 948 ± 161 m (*n* = 7 bats; Table 14.1). There were no significant differences between sexes in LAX (Kruskal-Wallis chi-squared, *P* = 0.48). Adult females had median values of LAX larger than adult males (Fig. 14.6a). Nevertheless, males had highly variable movements and sometimes moved long distances from their tents (e.g., bat M2 in Table 14.1).

The mean PAC within 100 m from tents was 25.2 ± 11.9 m (*n* = 7 bats; Table 14.1). For adult males, 46.2 ± 24.2 % of all total activity locations from telemetry were within 100 m of their tents, while for adult females this represented only 9.4 ± 3.0 % of all activity points (Fig. 14.6b). There was a significant difference between the percentages of activity as a function of distance from tents between sexes with males active closer to tents (TukeyHSD test, *P* = 0.05).

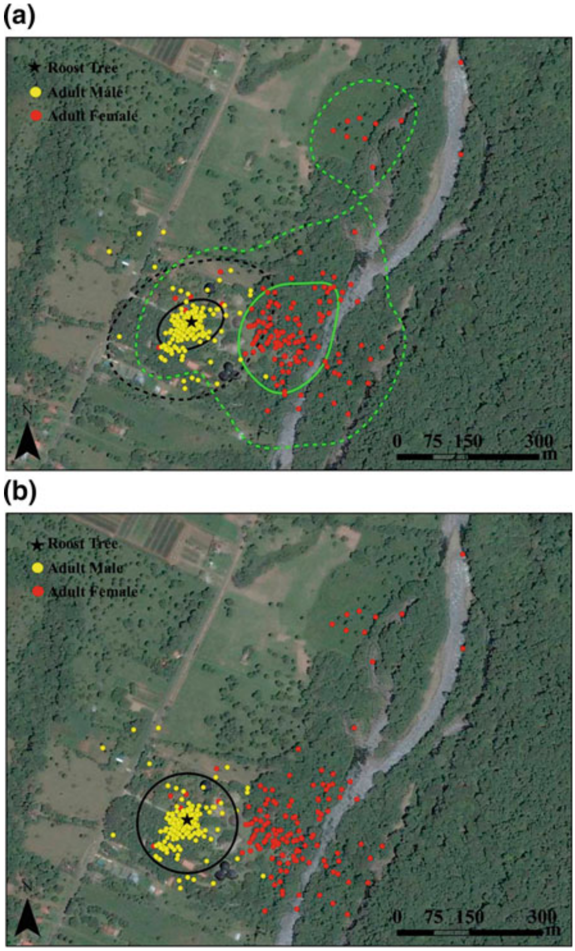


Fig. 14.5 **a** 95 % FR kernels (dotted lines) and 50 % CUA kernels (solid lines) of two representative bats occupying the same tent, male 2 and female 4. **b** Scatter plot of FR of male 2 and female 4 depicting the strong tendency to remain close to the tent by this male. The circle around the tent location is a 100 m radius

Uroderma foraged in a variety of habitats as follows (Table 14.2): riparian (42.7 ± 9.9 % of all telemetry positions), gardens (31.3 ± 11.6 %), closed canopy upland forests (21.9 ± 5.4), and pastures (4.1 ± 0.9 %). Females showed significantly higher percentage of activity (61.7 ± 4.9 % of total locations) than males (17.4 ± 8.7 % of total locations) in riparian forest (one-way ANOVA TukeyHSD test, $P = 0.005$ and Fig. 14.7). The use of gardens also differed significantly between sexes (TukeyHSD test, $P = 0.01$; Fig. 14.7). Adult males used gardens (54.8 ± 21.2 % of total locations) more than females (13.7 ± 1.5 %). There was no significant difference between females and males in the use of closed canopy upland forests (TukeyHSD test, $P = 0.69$) or pastures (TukeyHSD test, $P = 0.41$).

Four adult males and three adult females were used during captive observation of fruit manipulation. We recorded 12 feeding observations for *F. insipida* (males = 5 and females = 7) and 21 feeding observations for *F. citrifolia*

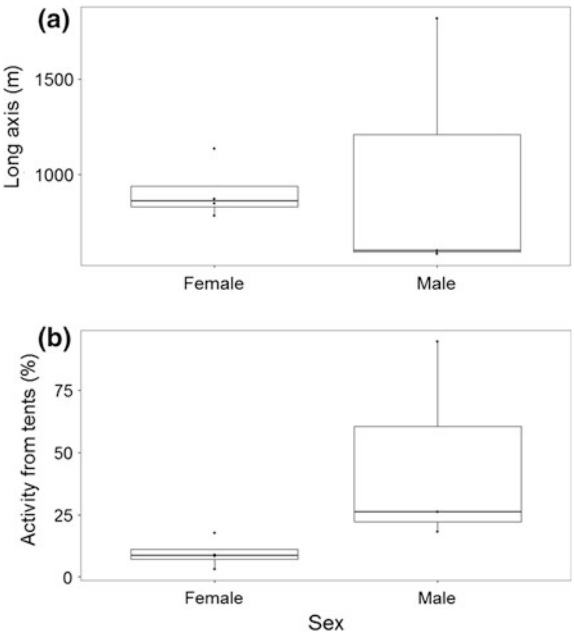


Fig. 14.6 Median (quartiles and range) of the LAX (**a**) and the percentage of activity ≤100 m from tents (**b**) for male and female *U. convexum* at Sarapiquí

Table 14.2 Habitat use of *U. convexum* at Sarapiquí

Bat I.D.	Telemetry positions (n)	% of Telemetry positions by habitat			
		Riparian	Forest	Pasture	Garden
M2	423	0.5	0.5	1.9	97.1
M3	103	29.1	35.9	1.0	34.0
M4	111	22.5	37.9	6.3	33.3
F3	144	54.9	27.1	3.4	14.6
F4	160	60.6	18.8	4.3	16.3
F5	170	55.3	27.1	8.2	9.4
F6	125	76.0	6.4	3.2	14.4
Mean ± SE	176.6 ± 42.1	42.7 ± 9.9	21.9 ± 5.4	4.06 ± 0.9	31.3 ± 11.5

(males = 2 and females = 19). Bats usually consumed more than 50 % of the wet mass of all figs before discarding them (51.6 ± 2.6 for *F. insipida* and 57.5 ± 3.6 for *F. citrifolia*). However, entire *F. insipida* were consumed in 43.5 ± 3.7 min (n = 12), in contrast to 4.8 ± 0.2 min for *F. citrifolia* (n = 21) (Fig. 14.8a, b).

Statistical analyses (2-way ANOVAs) indicated no significant differences in processing time of *F. insipida* (F = 0.501, $P \geq 0.49$; Fig. 14.8a) or *F. citrifolia* (F = 0.964, $P \geq 0.34$; Fig. 14.8b) among sexes. No significant differences were found neither in the interaction between sex and wet fruit mass for *F. insipida* (F = 0.065, $P = 0.81$) or for *F. citrifolia* (F = 0.366, $P = 0.55$).

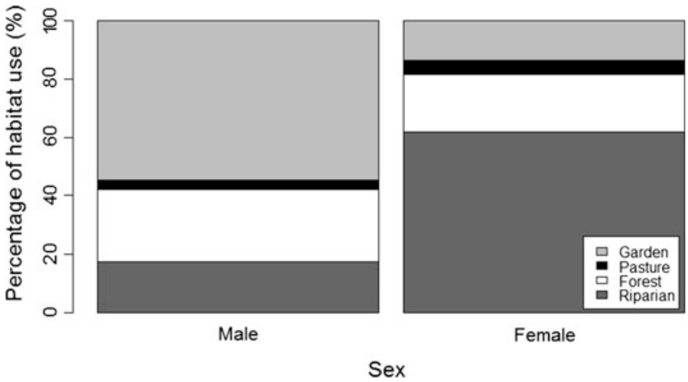
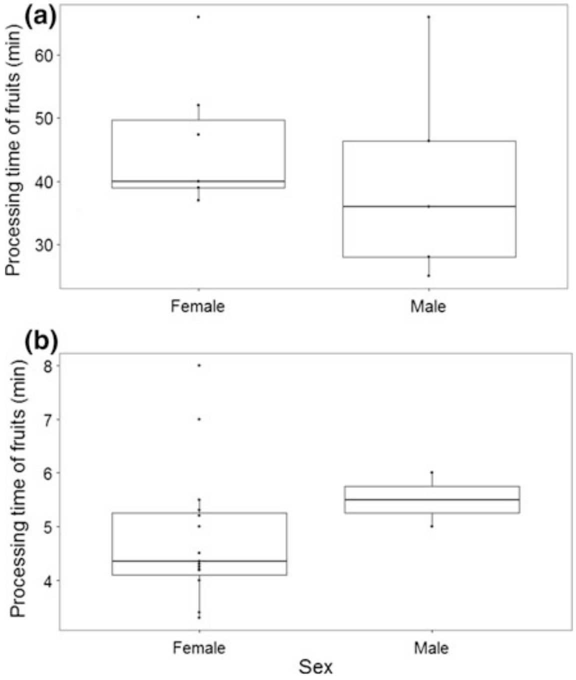


Fig. 14.7 Percent habitat use for adult males and female *U. convexum* at Sarapiquí

Fig. 14.8 Median (quartiles and range) of the consumption time of ripe fruits of *F. insipida* (**a**) and *F. citrifolia* (**b**) by *U. convexum* at Sarapiquí



We found 321 large seeds representing 6 plant species in our quadrats that showed signs of manipulation by bats (e.g, tooth marks and removal of pulp/arils) (Table 14.3). All large seeds dispersed by *U. convexum* represented either dicot or monocot tree species including palms and were associated with different forest successional stages (Table 14.3). *Spondias radlkoferi* (*n* = 154, 48.0 %) and *Calophyllum brasiliense* (*n* = 148, 46.1 %) accounted for most of the large seeds in

Table 14.3 List of plant species in the diet of *U. convexum* at Sarapiquí from seeds found under tents and plants visited by radiotagged bats

Family	Species	Detection*	Number of seeds	Associated habitat (s)	Life form
Anacardiaceae	*Spondias radlkoferi*	FR	154	Mature and secondary forest	Tree
Calophyllaceae	*Calophyllum brasiliense*	FR	148	Mature forest	Tree
Sapotaceae	*Pouteria* sp	FR	12	Mature forest	Tree
Humiricaceae	*Sacoglotys trichogyna*	FR	4	Mature forest	Tree
Arecaceae	*Astrocaryum alatum*	FR	2	Mature forest	Palm
Simaroubaceae	*Simarouba glauca*	FR	1	Mature and secondary forest	Tree
Moraceae	*Ficus insipida*	T	–	Mature and secondary forest	Tree
Moraceae	*Ficus citrifolia*	T	–	Mature and secondary forest	Tree
Moraceae	*Ficus popenoei*	T	–	Mature and secondary forest	Tree
Cecropiaceae	*Cecropia* sp	FR	–	Secondary forest	Tree
Solanaceae	*Solanum* sp	FR	–	Secondary forest	Shrub

**FR* Feeding roost; *T* Feeding tree

quadrats under tents (Table 14.3). All remaining seed species represented ≤4 % of total seeds. We qualitatively documented small-seeded plants in the diet of *U. convexum* both during visual inspections in the activity areas of radio-tagged bats and from seeds dropped by bats in quadrats placed under tents.

14.5 Discussion

Males of several tropical bat species are demonstrated to fight for dominance to secure access to females, either directly by defending groups of females or indirectly by monopolizing resources (Kerth 2008). For example, in both *A. jamaicensis* and *Saccopterix bilineata*, dominant males attack male intruders resulting in higher paternity success for these males within their own harem than do subordinate males which sometimes are tolerated in the harem, or satellite males which form separate roosting groups (Nagy et al. 2007; Ortega et al. 2003). In this context, our result indirectly support the hypothesis of male tent defense proposed by Kunz and McCracken (1996), and at least for the tent-making bat species *U. convexum*, we were able to confirm all of our predictions. It seems like the differences found between male and female behavior in FR, PAC and habitat use were influenced by the harem social system present in this species.

Our first and second prediction was supported by the differences in the foraging range and percentage of activity within and beyond 100 m away from the day roosts calculated for both sexes; with females showing larger foraging areas than males and significantly more activity away from the imaginary 100 m radius circle around tents during nightly foraging periods. In contrast, tent occupying males, when possible often would forage primarily on fruiting trees within 100 m of the tent. Much of the activity of the adult males was associated with anthropogenic gardens where tents in *C. nucifera* and *Musa* spp. usually are located. Our field observations and radiotracking data confirmed that adult males of *U. convexum* often carried fruit back to the tent or a foliage perch within view of their tent, contrasting to the behavior of adult females that generally only return to tents after foraging is concluded each night. With respect to our third prediction, we identified that although the general pattern of adult males was to restrict their movements close to their roosts, spatio-temporal changes in the availability of food resources can influence the movements of bats, potentially forcing the individuals to fly larger distances in order to get food, consequently increasing the size of their foraging range. This situation was confirmed with our tagged bats M3 and M4, which showed larger foraging ranges and less percentage of activity close to the tents than individual M2. Despite this, these individuals were more restricted to their roosts than all females monitored, in addition that we were able to confirm that they usually return during the night to the roosting area, probably in order to monitoring their roosts.

Regardless of the size of foraging range, monthly activity of *U. convexum* was concentrated in very small core-use areas, which change as fruiting trees sequentially produce ripe crops (Table 14.1). These small areas reflected the abundance, nutritional quality (especially high in calcium), and asynchronous fruiting of fig trees throughout the year in tropical forests (Bonaccorso 1979; Shanahan et al. 2001).

Regarding the role of bats as seed disperser, it seems that *U. convexum* is a habitat generalist and individuals frequently moved through several habitats within a night while foraging (Fig. 14.7, Table 14.2). At Sarapiquí, these bats used all four of the major habitat classes defined by us from land cover maps and moved between several feeding trees, from fruiting trees to night feeding roosts, and to and from its tent in the course of a night, effectively transported seeds well beyond the canopy of parent trees. Seed dispersal by *U. convexum* included many disturbed and mature natural habitats. Bats dispersed both small-seeded species while flying and deposited under feeding roosts and tents, as well as large-seeded plants deposited almost exclusively under roosts and tents (Rodríguez-Herrera et al. 2007).

At more specific level, it seems that sex differentiation influences the outcomes of the seed dispersal process carried out by *U. convexum*, partially confirming our fourth prediction. Both sexes used the four categories of habitat, consequently dispersing seeds in all these areas, nevertheless the percentage of activity differed between males and females, especially for those habitats classified as riparian and gardens (Fig. 14.7). Riparian habitats were used more than any other habitat by females and include many fruiting trees found in the diet of *U. convexum*. Direct observations confirmed frequent riparian habitat visitation of adult females F3 and F6 at *F. insipida* and *F. popenoei* having ripe figs.

The probability of finding *U. convexum* presence is highly associated with microhabitat variables, and with the presence of coconut palms (Sagot et al. 2013). In fact, all of the tents occupied by tagged individuals were located in gardens, and many of the native fruiting trees included in the diet of this bat species (Table 14.3) also can be found in this habitat. For example, one *F. citrifolia* tree frequently visited by bats M1, M2 and F2 was located in a garden < 10–20 m from several tents. The abundance of coconut palms and bananas commonly used to construct tents combined with the food resources probably influenced the high amount of activity of *U. convexum* in this anthropogenic environment. Higher levels of activity of adult males on this habitat (Fig. 14.7) were expected due to the tent defense behavior that restricted the movements of individuals to areas close to their roosts.

In the case of pastures and canopy upland forest, there were no evident differences between the percentages of activity of both sexes. Pasture was the habitat least visited by *U. convexum* and was mostly used for transit between other habitats. However, bats occasionally visited remnant fruiting trees in this habitat for feeding. Because phyllostomid bats create a seed rain, particularly of small-seeded species (e.g., *Ficus* spp., *Cecropia* spp., *Solanum* spp.) by defecating while flying (Arteaga et al. 2006) they assist the regeneration of abandoned pasture with seed rain from forests. On the other hand, high densities of food availability in the upland closed canopy forests is expected to be one of the most important variables influencing the movements of individuals within this habitat, especially considering that some plant species found in the diet of *U. convexum* are typical of mature forests (Table 14.3). Phyllostomid bats facilitate the reproductive success of plants in both highly disturbed areas and closed forest habitats, favor the maintenance of plant diversity, and make possible the dispersion of plant species across landscapes both through seed (and pollen) translocation (Ávila-Cabadilla et al. 2014; Vleut et al. 2013).

Finally, observations of fruit manipulation showed that captive *U. convexum* handling time for consumption of fruits was highly dependent of fig size and that there was no difference among sexes. Time invested by *U. convexum* in handling large fruits (i.e., *F. insipida*) was higher than time invested in small fruits (i.e., *F. citrifolia*). Independent of the time invested in feeding on a fruit, *U. convexum* frequently consumed a high percentage of total fruit mass (≥ 50 %) for both *F. insipida* and *F. citrifolia*. Heer et al. (2010) demonstrated that *Artibeus jamaicensis* positively influences the germination success of the fig seeds ingested by removing pulp from around seeds in the digestion process. The consumption of fig fruits by *U. convexum* likely also helps *F. insipida* and *F. citrifolia* seeds to have enhanced germination success. Fruits with small seeds generally contain large numbers of seeds (e.g., *F. citrifolia* have a mean of 274 ± 13.9 seeds per ripe syconium; range = 202–314; $n = 8$). Considering that *U. convexum* was able to eat an entire ripe *F. citrifolia* fig in 4.8 ± 0.3 min, one bat potentially will disperse several thousand small seeds in multiple habitats within their foraging areas each night.

Our results demonstrated that, independent of the sex, *U. convexum* constantly move seeds from trees located in both mature and successional upland and riparian forests to highly disturbed areas such as gardens, pastures, and other agricultural landscapes. Large movements (LAX) of some individuals (i.e., 1817 m), in addition that some of our radio-tagged bats (F1 and F2) moved even farther when radio contact was lost no doubt facilitate long-distance dispersal, especially for small-seeded plant species. In contrast, loyalty to a few specific feeding roosts probably reduces the efficiency of the dispersal performed by *U. convexum* on large-seeded plants considering that the localities where the seeds are dropped are few. Nevertheless, survival rates of the seeds under these bat roosts are not documented as yet, and based on field observations, there are some level of seed germination under tents and feeding roosts in disturbed habitats, which results in the positive establishment of seedlings of some plants such *Cecropia* spp, *C. brasiliense,* and *S. radlkoferi.*

In conclusion, our study is the first in analyze the nightly behavior of a Neotropical tent-making bat species in the context of the hypothesis proposed by Kunz and McCracken (1996). Although we were not be able to document tent construction by males of *U. convexum*, our data suggests that activity patterns of adult males seems to respond to the defense of roosting resources. Differences in activity patterns of both sexes also influenced the role of bats as seed dispersers. Larger range of movements and the plasticity in habitat use of adult females will result in differences in the distance of the seed dispersal (females moved greater distances) and in the proportion of time expended in the habitats where the seeds will be deposited. Social behavior of *U. convexum* in conjunction with the quality of seed dispersal bears interesting potential for further testing among the variety of tent-constructing bats in Central America.

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References

Anthony ELP (1988) Age determination in bats. In: Kunz TH (ed) Ecological and behavioral methods for the study of bats, 2nd edn. The John Hopkins University Press, Baltimore, MD, pp 47–58

Arteaga LL, Aguirre LF, Moya MI (2006) Seed rain produced by bats and birds in forest islands in a Neotorpical savana. Biotropica 38:718–724

Audet D (1990) Foraging behavior and habitat use by a gleaning bat *Myotis myotis* (Chiroptera: Vespertilionidae). J Mamm 71:420–427

Ávila-Cabadilla LD, Stoner KE, Nassar JM, Espírito-Santo MM, Alvarez-Añorve MY, Aranguren CI, Henry M, González-Carcacía J, Dolabela L, Sanchez-Azofeifa GA (2014)

Phyllostomid bat occurrence in successional stages of Neotropical dry forests. PLoS ONE 9(1): e84572. doi:10.1371/journal.pone.0084572

Barbour T (1932) A peculiar roosting habit of bats. Quart. Rev. Biol 7:307–312

Baker RJ, Clark CL (1987) Uroderma bilobatum. Mamm Species 279:1–4

Balasingh J, Koilraj K, Kunz TH (1995) Tent construction by the frugivorous bat *Cynopterus sphinx* (Chiroptera: Pteropodidae) in southern India. Ethology 100:210–229

Bonaccorso FJ (1979) Foraging and reproductive ecology in a Panamanian bat community. Bull Florida State Mus, Biol Sci 24:359–408

Bonaccorso FJ, Todd CM, Miles AC, Gorresen PM (2015) Foraging movements of the endangered Hawaiian hoary bat, *Lasiurus cinereus semotus* (Chiroptera: Vespertilionidae). J Mammal 96(1):64–71

Brooke AP (1990) Tent selection, roosting ecology and social organization of the tent-making bat, *Ectophylla alba*, in Costa Rica. J Zool (London) 221:11–19

Chaverri G, Kunz TH (2006) Roosting ecology of the tent-roosting bat *Artibeus watsoni* (Chiroptera: Phyllostomidae) in southwestern Costa Rica. Biotropica 38:77–84

Dechmann DKN, Kalko EKV, Kerth G (2004) Ecology of an exceptional roost: energetic benefits could explain why the bat *Lophostoma silvicolum* roosts in active termite nests. Evol Ecol Res 6:1037–1050

ESRI (2010) ArcGIS 10.0: Geographic Information System. Environmental Systems Research Institute, Redlands, California. http://www.esri.com/

Fleming TH (1988) The short-tail fruit bat: a study in plant animal interactions. The University of Chicago Press, Chicago, IL

Fleming TH, Heithaus ER (1981) Frugivorous bats, seed shadows, and the structure of tropical forests. Biotropica (Reproductive botany supplement) 13:45–53

Fleming TH, Hooper ET, Wilson ED (1972) Three Central American bat communities: structure, reproductive cycles, and movements patterns. Ecology 53:555–569

Gardner AL (1977) Feeding habitats. In: Baker RJ, Jones JK Jr, Carters DC (eds) Biology of bats of the new world family Phyllostomatidae, Part II. Spec Pub, Texas Tech Univ Mus, p 293–350

Gianini NP, Kalko EKV (2004) Trophic structure in a large assemblage of phyllostomid bats in Panama. Oikos 105:209–220

Goodwin GG, Greenhall AM (1961) A review of the bats of Trinidad and Tobago. Descriptions, rabies infection and ecology. Bull Am Mus Nat Hist 122:187–302

Gorchov DF, Cornejo F, Ascorra C, Jaramillo M (1993) The role of seed dispersal in the natural regeneration of rain forest after stripcutting in the Peruvian Amazon. Vegetatio 108:339–349

Handley CO Jr, Gardner AL, Wilson DE (1991) Food habits. In: Handley CO Jr, Wilson DE, Gardner AL (eds) Demography and natural history of the common fruit bat, *Artibeus jamaicensis*, on Barro Colorado Island, Panama. Smithsonian Institution Press, Washington, DC, pp 141–146

Heer K, Albrecht L, Kalko EKV (2010) Effects of ingestion by neotropical bats on germination parameters of native free-standing and strangler figs (*Ficus* sp., Moraceae). Oecologia 163:425–435

Holdridge LR (1967) Life zone ecology. Centro Científico Tropical, San José, Costa Rica

Kerth G (2008) Causes and consequences of sociality in bats. Bioscience 58:737–746

Kunz TH (1982) Roosting ecology of bats. In: Kunz TH (ed) Ecology of bats. Plenum, New York, pp 1–56

Kunz TH, Lumsden LF (2003) Ecology of cavity and foliage roosting bats. In: Kunz TH, Fenton MB (eds) Bat Ecology. The University of Chicago Press, Chicago, IL, pp 3–90

Kunz TH, McCracken GF (1996) Tents and harems: apparent defence of foliage roosts by tent-making bats. J Trop Ecol 12:121–137

Kunz TH, Allgaier AL, Seyjagat J, Caligiuri R (1994) Allomaternal care: helper-assisted birth in the Rodrigues fruit bat, *Pteropus rodricensis* (Chiroptera, Pteropodidae). J Zool 232:691–700

LaVal RK, Rodríguez-Herrera B (2002) Murciélagos de Costa Rica. Instituto Nacional de Biodiversidad, Santo Domingo, Heredia

Law BS, Lean M (1999) Common blossom bats (*Syconycteris australis*) as pollinators in fragmented Australian tropical rainforest. Biol Conserv 91:201–212

Lewis SE (1992) Behavior of Peter's tent-making bat, *Uroderma bilobatum*, at maternity roosts in Costa Rica. J Mammal 73:541–546

Lobova TL, Geiselman C, Mori SA (2009) Seed dispersal by bats in the Neotropics. The New York Botanical Garden Press, Bronx, New York

Lyon MW (1902) Description of a new phyllostome bat from the Isthmus of Panama. Proc Biol Soc Wash 15:83–84

Mantilla-Meluck H (2014) Defining species and species boundaries in Uroderma (Chiroptera: Phyllostomidae) with a description of a new species. Occas Pap Texas Tech Univ Mus 325:1–25

McDade LA, Bawa SL, Hespenheide HA, Hartshorn GS (1994) La Selva, ecology and natural history of a Neotropical rain forest. The University of Chicago Press, Chicago, IL

Melo FPL, Rodríguez-Herrera B, Chazdon RL, Medellin RA, Ceballos GG (2009) Small tent-roosting bats promote dispersal of large-seeded plants in a Neotropical forest. Biotropica 41:737–743

Nagy M, Hecke G, Voigt CC, Mayer F (2007) Female-biased dispersal and patrilocal kin groups in a mammal with resource-defence polygyny. Proc Roy Soc B 274:3019–3025

O'Donnell CFJ (2001) Home range and use of space by *Chalinolobus tuberculatus*, a temperate rainforest bat from New Zealand. J Zool (London) 253:253–264

Ortega J, Maldonado JE, Wilkinson GS, Arita HT, Fleischer RC (2003) Male dominance, paternity, and relatedness in the Jamaican fruit-eating bat (*Artibeus jamaicensis*). Mol Ecol 12:2409–2415

R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, http://www.R-project.org/

Rodgers AR, Carr AP (1998) The home range extension for ArcView. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario

Rodríguez-Herrera B, Wilson DE (1999) Lista y Distribución de las Especies de Murciélagos en Costa Rica. Occasional Papers in Conservation Biology. Conserv Int 5:1–29

Rodríguez-Herrera B, Medellín RA, Gamba-Ríos M (2006) Tent building by female *Ectophylla alba* (Chiroptera: Phyllostomidae) in Costa Rica. Acta Chiropterol 8:557–560

Rodríguez-Herrera B, Medellin RA, Timm RM (2007) Murciélagos Neotropicales que acampan en hojas: Neotropical tent-roosting bats. Instituto Nacional de Biodiversidad, Santo Domingo, Heredia

Rodríguez-Herrera B, Ceballos GG, Medellín RA (2011) Ecological aspects of the tent building process by *Ectophylla alba* (Chiroptera: Phyllostomidae). Acta Chiropterol 13:365–372

Rothenwöhrer C, Becker NI, Tschapka M (2010) Resource landscape and spatio-temporal activity patterns of a plant-visiting bat in a Costa Rican lowland rainforest. J Zool (London) 283:108–116

Sagot M, Rodríguez-Herrera B, Stevens RD (2013) Macro and microhabitat associations of the Peters' tent-roosting bat (*Uroderma bilobatum*): human-induced selection and colonization?. Biotropica 0:1–9

Seaman DE, Millspaugh JJ, Kernahan BJ, Brundige GC, Raedeke KJ, Gitzen RA (1999) Effects of sample size on kernel foraging range estimates. J Wildl Manag 63:739–747

Shanahan M, So S, Compton SG, Corlett R (2001) Fig-eating by vertebrate frugivores: a global review. Biol Rev Camb Philos Soc 76:529–572

Sikes RS, Gannon WL, and The Animal Care and Use Committee of the American Society of Mammalogists (2011) Guidelines of the American Society of Mammalogists for the use of wild mammals in research. J Mammal 92:235–253

Storz JF, Bhat HR, Kunz TH (2001) Genetic consequences of polygyny and social structure in an Indian fruit bat, *Cynopterus sphinx*, I: inbreeding, outbreeding, and population subdivision. Evolution 55:1215–1223

Timm RM, Lewis SE (1991) Tent construction and use by *Uroderma bilobatum* in coconut palms (*Cocos nucifera*) in Costa Rica. Bull Am Mus Nat Hist 206:251–260

Vleut I, Levy-Tacher SI, de Boer WF, Galindo-González J, Vazquez LB (2013) Tropical secondary forest management influences frugivorous bat composition, abundance and fruit consumption in Chiapas, Mexico. PLoS ONE 8(10):e77584. doi:10.1371/journal.pone.0077584

Waldien DL, Hayes JP (2001) Activity areas of female long-eared *Myotis* in coniferous forests in western Oregon. Northwest Sci 75:307–314

Waters D, Jones G, Furlong M (1999) Foraging ecology of Leisler's bat (*Nyctalus leisleri*) at two sites in southern Britain. J Zool (London) 249:173–180

Winkelmann JR, Bonaccorso FJ, Strickler TL (2000) Home range of the common blossom bat, *Syconycteris australis*. J Mammal 81:408–414