

Foraging and Roosting Behaviour of the Fringe-Lipped Bat, *Trachops cirrhosus*, on Barro Colorado Island, Panamá

Author(s): Patricia L. Jones, Frank Hämsch, Rachel A Page, Elisabeth K. V. Kalko and M. Teague O'Mara

Source: Acta Chiropterologica, 19(2):337-346.

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

<https://doi.org/10.3161/15081109ACC2017.19.2.010>

URL: <http://www.bioone.org/doi/full/10.3161/15081109ACC2017.19.2.010>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Foraging and roosting behaviour of the fringe-lipped bat, *Trachops cirrhosus*, on Barro Colorado Island, Panamá

PATRICIA L. JONES^{1,2,7}, FRANK HÄMSCH³, RACHEL A PAGE², ELISABETH K. V. KALKO^{2,4},
and M. TEAGUE O'MARA^{2,5,6}

¹Department of Biology, Bowdoin College, 6500 College Station, Brunswick ME 04011-8465, USA

²Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, República de Panamá

³Department of Biology, University of Tübingen, Auf der Morgenstelle 32, 72076 Tübingen, Germany

⁴Institute of Experimental Ecology and Conservation Genomics, University of Ulm, Albert-Einstein Allee 11, D-89069 Ulm, Germany

⁵Department of Migration & Immuno-ecology, Max Planck Institute for Ornithology, Am Obstberg 1, 78315 Radolfzell, Germany

⁶Department of Biology, University of Konstanz, Universitätsstraße 10, 78464 Konstanz, Germany

⁷Corresponding author: E-mail: pjones3@bowdoin.edu

The Neotropical fringe-lipped bat, *Trachops cirrhosus*, is a generalist predator that hunts frogs and insects by homing in on their mating calls. Although research has examined cognition and prey preferences of bats in captivity, little is known of the foraging or roosting behaviour of this species in the wild. We radio tracked six *T. cirrhosus* individuals on Barro Colorado Island, Panamá. Bat day roosts were all in hollow cashew trees, *Anacardium excelsum*, in mixed sex groups of three to five *T. cirrhosus* individuals, with frequent roost switching. Radio tracked individuals flew an average of 218 ± 227 m from their day roosts to 12.0 ± 10.17 ha foraging areas (50% utilization distribution [UD] kernels = areas where bats spent 50% of their time as estimated from a probability distribution). These 50% UD kernels were less than 10% of their average total range use, but larger than previously reported for *T. cirrhosus*. Radio tracked individuals overlapped in 50% UD kernel foraging areas by only 2.1 ± 5.9 % on average. Foraging behaviour consisted predominantly of short sally flights of less than one minute, indicating bats were likely perch hunting. Bats were more frequently in flight, and had longer flight durations, at the beginning of the night and just before dawn than throughout the rest of the night. These data provide insight into the foraging behaviour of *T. cirrhosus* in the wild, that is a species fast becoming a model system of cognition in captivity.

Key words: Barro Colorado Island, Chiroptera, Brownian bridge, movement ecology, roosting behaviour, telemetry, *Trachops cirrhosus*, social learning

INTRODUCTION

The Neotropical fringe-lipped bat, *Trachops cirrhosus* (Spix, 1823), is a member of the leaf-nosed bats (Phyllostomidae), and is the sole species in the genus *Trachops*. The range of *T. cirrhosus* extends from Mexico to Brazil (Cramer *et al.*, 2001), although this group may encompass as many as nine subspecies (Clare *et al.*, 2011). *Trachops cirrhosus* is a gleaner predator that consumes a wide variety of insect and vertebrate prey (Bonato *et al.*, 2004; Giannini and Kalko, 2004). Flight cage observations indicate that it is a perch-hunter that predominantly relies on prey-emitted cues such as prey mating calls to initiate attack (reviewed in Page and Jones, 2016). It is particularly well known for its eavesdropping on frog sexual advertisement calls (Tuttle and Ryan,

1981), earning it the nickname, the ‘frog-eating bat’. Its behaviour of eavesdropping on frog calls has made *T. cirrhosus* a model for examining how predation can be a selective force on sexual advertisement signals of prey (Ryan and Tuttle, 1982; Akre and Ryan, 2010; Trillo *et al.*, 2012; Halfwerk *et al.*, 2014a, 2014b). *Trachops cirrhosus* has also become the focus of studies of animal cognition as it is a fast learner (Page and Ryan, 2005), can learn socially from interacting with other bats (Page and Ryan, 2006; Jones *et al.*, 2013), and integrates cues across multiple modalities (Halfwerk *et al.*, 2014a, 2014b). In many ways *T. cirrhosus* seems to be unusual among bats in its cognitive capabilities, perhaps due to natural selection for eavesdropping behaviour, which requires bats to identify a variety of prey using their species-specific sexual advertisement calls.

Flight cage experiments have illuminated much about the sensory and cognitive biology of *T. cirrhosus*, but in contrast, surprisingly little is known about the ecology and behaviour of this bat species in the wild. Throughout its range, *T. cirrhosus* has been captured in a variety of habitat types, and roosts predominantly in hollow trees, but roosts have also been found in caves and abandoned human-made structures such as buildings and culverts (Cramer *et al.*, 2001). The only published radio tracking study of *T. cirrhosus* followed two individuals over two weeks on Barro Colorado Island in Panamá (Kalko *et al.*, 1999). This study found that these two bats had low fidelity to their day roosts, but high fidelity to 3–4 ha foraging sites around streams. Throughout the night bats made short flights, mostly less than a minute long, with some longer flights upon emergence at the beginning of the night. The authors suggested that the long flights at the beginning of the night were when bats were foraging for frogs as this was the time when frogs were frequently calling (Kalko *et al.*, 1999).

We investigated the roosting behaviour, foraging areas, and activity patterns of six *T. cirrhosus* on Barro Colorado Island (BCI) over two months. We tested four hypotheses about the ecology and behaviour of this bat species: (i) *T. cirrhosus* have low fidelity to day roosts because it is known that our population roost predominately in tree cavities (Kalko *et al.*, 1999), and tree cavity roosters switch roosts often (Lewis, 1995, Trousdale *et al.*, 2008); (ii) *T. cirrhosus* exhibit ‘fission-fusion’ style roosting dynamics, in which groups split apart and later reform, because low day roost fidelity would disrupt stable social groups; (iii) *T. cirrhosus* have relatively large foraging areas for a tropical bat and the behaviour of eavesdropping on frog calls may allow them to locate prey over much larger distances than by echolocation in dense forest because lower frequency sounds in the audible range transmit further than higher frequency sounds (Wiley and Richards, 1978, Richards and Wiley, 1980); (iv) *T. cirrhosus* would exhibit activity patterns in accordance with

a perch hunting strategy (i.e. predominantly short sally flights interspersed with long stationary periods) based on previous study (Kalko *et al.*, 1999).

MATERIALS AND METHODS

Habitat and Animals

We radio tracked *T. cirrhosus* from March 12th to May 8th, 1997 (dry season to the beginning of the rainy season) on BCI in Panamá (9°09'N, 79°51'W). We captured *T. cirrhosus* in mistnets at night either around streams or outside known roosts. We fitted six adults (4 ♀♀ and 2 ♂♂ — Table 1) with radio transmitters (BD-2AP, Holohil Systems Ltd., Carp, Ontario, Canada). We trimmed the fur on the centre of the back between the shoulder blades as short as possible, cleaned the skin and the transmitter with alcohol, attached the transmitter using a tissue adhesive (Skin-Bond®), and held it in place until dry (ca. 20 min). The transmitters weighed 1.5–1.6 g, about 5% of the body mass of *T. cirrhosus*, which is within the recommended range for bats (Aldridge and Brigham, 1988; O'Mara *et al.*, 2014b).

Tracking

We tracked bats for a total of 28 days (including 15 full nights (18:00–6:30 hrs), totalling 342 hrs of contact data. We tracked one bat per night by triangulating radio signals using a five-arm Yagi antenna attached to a Yaesu (FT-290 R/II) receiver and Wagener (Type 150 H 10R) antenna amplifiers. We collected individual compass bearings every five minutes from two tracking sites. Due to the topography and vegetation of BCI, the maximum detection range was 300–500 m.

We calculated geographic locations for each fix from the bearing data in the ‘geosphere’ package (Hijmans, 2016) in R 3.2.3 (R Core Team, 2015) and visualized them with ‘ggmap’ (Kahle and Wickham, 2013). We then calculated 95% minimum convex polygons for each bat in ‘adehabitatHR’ (Calenge, 2006). To better test the overlap of the intensity of range use by our tracked individuals we estimated overlap of utilization distributions. We first calculated dynamic Brownian bridge movement models for each individual in ‘move’ (Kranstauber *et al.*, 2012) using an error of 20 m, a time step of five minutes, and default window and margin sizes. This method has the advantage of incorporating both the temporal structure of the data and a dynamically estimated variance to further estimate the likely movement paths the individuals took to their measured position (Horne *et al.*, 2007). We did this for each night of activity separately and then summed the results. We used these models to calculate the proportion of overlap of utilization distributions

TABLE 1. Day roost fidelity of radiotracked bats of *T. cirrhosus* in Barro Colorado Island, Panamá

Roost	Tree diameter at breast height (DBH)	F1	F2	F3	F4	M1	M2
Balboa	170	–	March 31 –April 16	April 10 –April 18	March 31 –April 16	–	–
Chapman	172	April 30 –May 4	–	–	–	–	–
Shannon	175	–	March 12 –March 30	–	March 29 –March 30	May 5 –May 14	March 26 –March 28

at the 50% and 95% kernels (areas where bats spent 50% and 95% of their time, respectively) in 'adehabitatHR'.

We measured activity as either flying or hanging/roosting using changes in the radio transmitter pulse rate modulated by a crystal oscillator in the transmitters. When hanging, the transmitter pulsed at 0.35–0.40 pulses s^{-1} and when flying the pulse rate increased to 0.75–0.80 pulses s^{-1} . We sampled activity once per minute. All location data are available for download at movebank.org (doi: 10.5441/001/1.15pq1m81). To evaluate how activity and flight durations and types were distributed across the night we used generalized linear mixed effects models in 'lme4' (Bates *et al.*, 2015) with bat identity as a random intercept. We compared nested models that differed by the fixed effect of interest using a likelihood ratio test (χ^2).

RESULTS

Roosting Behaviour

We located three of the day roosts used by the bats. We refer to the roosts by the valleys in which they were located: Shannon, Balboa and Chapman (Fig. 1). All of the day roosts were located in trunk cavities of wild cashew trees (*Anacardium excelsum*). Three of the radio tracked individuals changed their roosts during the observation period. Two females (F2 and F4) roosted together at Shannon

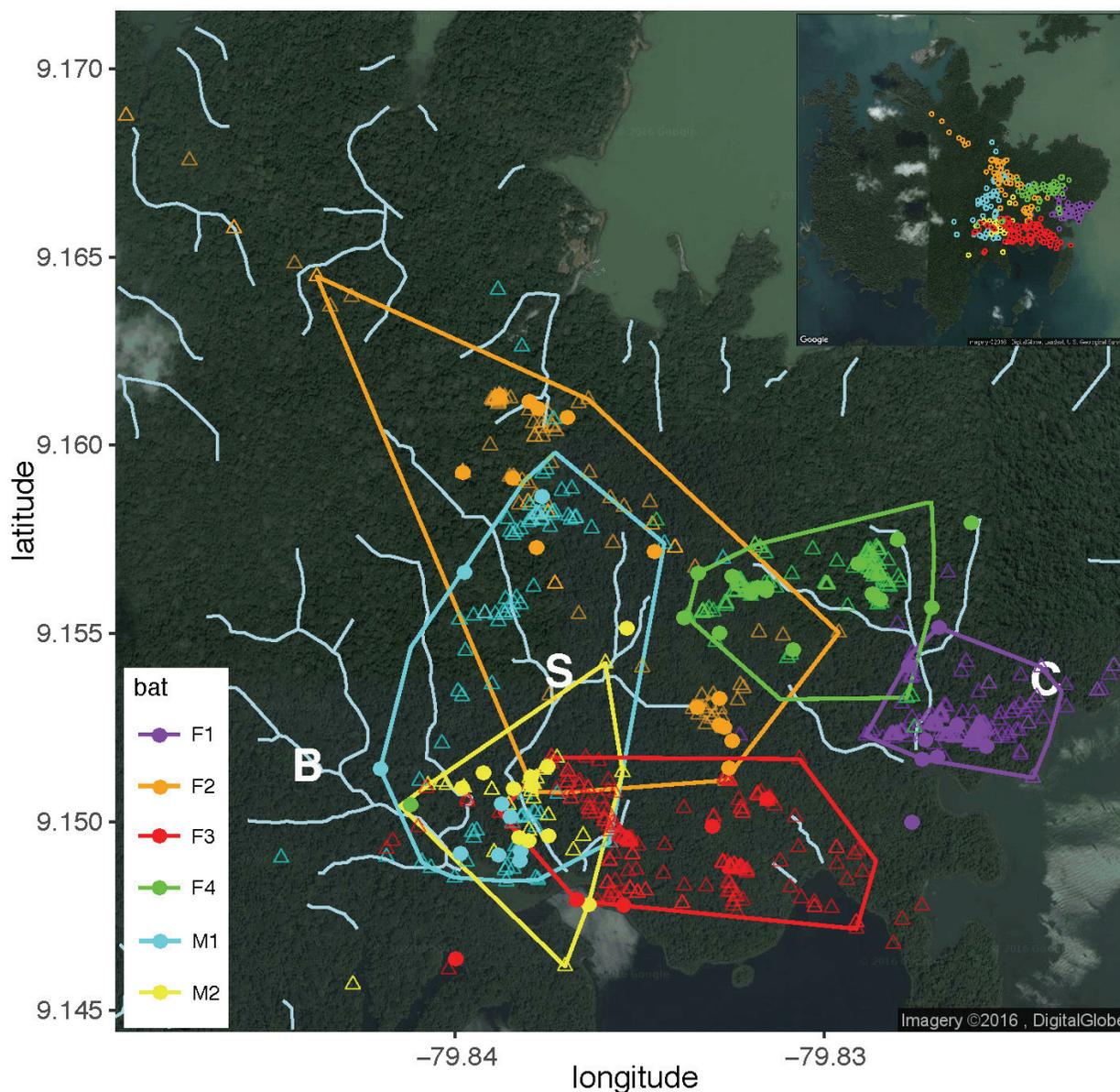


FIG. 1. Triangulated locations, activity at that location, and 95% MCP areas for each tracked *T. cirrhosus* on Barro Colorado Island (inset). Filled circles indicate locations where flying and open triangles show positions where bats were hanging. Individual bats and their 95% MCP are colour matched. Letters denote roost locations (B — Balboa, S — Shannon, C — Chapman). Stream locations are shown in light blue

Roost, and simultaneously switched to Balboa Roost (500 m away). Seventeen days later the same two females both left the Balboa Roost and moved to an unknown location (Table 1).

On four different days at the Shannon Roost and one day at the Balboa Roost we attempted to capture all of the bats within the roost to examine the social dynamics of roosting *T. cirrhosus*. We found between four and five individuals at Shannon Roost each day and three individuals at Balboa Roost. Captured groups included multiple individuals of both sexes in varying reproductive states: Shannon Roost on March 26th contained two pregnant females, a reproductive male, and a non-reproductive male; on March 29th it contained one juvenile female and three non-reproductive females; on April 22nd it contained two non-reproductive males and one reproductive male; and on May 8 it contained one pregnant female, two non-reproductive females, and two non-reproductive males. Balboa Roost on April 10 contained one pregnant female, one non-reproductive female, and one post-lactating female. These roosts were also used during the day by *Carollia perspicillata* and *Phyllostomus discolor*. We counted over 25 animals flying into Balboa roost. In Chapman Roost we observed over 30 bats (of multiple species) in one day hanging in small groups at different heights within the hollow trunk.

Home Ranges

The average home range size of *T. cirrhosus* in our study was 60.05 ± 34.27 ha using 95% minimum convex polygon (MCP), and 157.18 ± 141.13 ha using 95% utilization distribution (UD) estimated from dynamic Brownian bridges. The higher total area with dynamic Brownian bridges accounts for the transition probability between subsequent radio signal locations and the location error surrounding the space needed to move between locations. We

found large individual variation in home range size (Table 2 and Fig. 1), which was not a function of the number of nights observed ($F_{1,4} = 0.077$, $P = 0.80$). Home ranges of these bats were not exclusive and each bat overlapped with the range of one to four other radio tracked individuals (Table 3). All overlaps we report were only in space, not in time and space, because we did not track the bats simultaneously. On average, the 95% UD ranges of individual bats overlapped $13.4 \pm 23.8\%$.

Foraging Areas

Bats travelled an average of 218 ± 227 m from their day roosts to exploit foraging areas (50% UD kernels) that were 12.0 ± 10.17 ha, or less than 10% of their average total range use. Bats used multiple foraging areas throughout the night to find food (Fig. 2). The tracked bats did reuse foraging areas across tracking nights but not in a repeated or predictable pattern. The 50% UD kernel foraging areas overlapped between individuals by only $2.1 \pm 5.9\%$ on average (Table 3). Most bats therefore had exclusive foraging areas, with overlap only observed in the pairs F2-M1, and M1-M2, largely as a consequence of the central location of the areas of F2 and M1. In particular, the two females (F2 and F4) that roosted together had no overlap in 50% UD foraging areas, although note that they do overlap in 95% MCP home ranges (Fig. 1).

Activity Patterns

Sunset was at 18:29 for the full length of the tracking period (March 12 to May 8). Sunrise ranged from 6:28 on March 12th to 5:59 on May 8th. Bats emerged from their day roosts at between 18:24 and 19:20 and returned between 5:40 and 6:33 (Table 4). Bats did not return to their day roosts during the night and we saw no evidence of use of consistent night roosts. Activity monitoring of the

TABLE 2. Number of nights tracked, percentage of contact time, and foraging areas of radiotracked *T. cirrhosus* in Barro Colorado Island. MCP is minimum convex polygon and UD is the utilization distribution in hectares

Bat	Sex	Reproductive status	Mass (g)	N nights	% contact time	Number of locations	95% MCP	50% kernel UD	95% kernel UD
F1	♀	post-lactating	30.5	4	63.7	357	15.03	1.56	23.44
F2	♀	post-lactating	33.0	4	73.1	144	110.04	29.26	367.94
F3	♀	non-reproductive	35.0	8	74.7	447	60.35	16.90	134.46
F4	♀	non-reproductive	38.0	7	77.6	299	47.84	3.41	96.37
M1	♂	non-reproductive	28.0	4	66.8	192	87.74	12.38	288.98
M2	♂	reproductive	34.0	1	92.3	62	39.32	8.46	31.90
Mean			33.1 ± 3.5	4.7 ± 2.5	63.7 ± 10.0		60.05 ± 34.27	12.00 ± 10.17	157.18 ± 141.13

TABLE 3. Percent overlap of foraging ranges (50% UD) and home range (95% UD in parentheses) utilization distribution for each pair of *T. cirrhosus* in Barro Colorado Island. Bats have a mean foraging range overlap of $2.1 \pm 5.9\%$ and a home range overlap of $13.4 \pm 23.8\%$

Bat	F1	F2	F3	F4	M1	M2
F1	—	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
F2	0 (0)	—	0 (5.9)	0 (5)	11.8 (47.4)	0 (5.7)
F3	0 (0)	0 (19.5)	—	0 (0.5)	0 (12.5)	0 (2.7)
F4	0 (0)	0 (16.5)	0 (0.5)	—	0 (15)	0 (2.5)
M1	0 (0)	23.7 (62.5)	0 (5)	0 (6)	—	6.5 (11.6)
M2	0 (0)	0 (64.8)	0 (9.2)	0 (8.7)	19.8 (100)	—

bats indicated that an average 95% of the flights made by the six radio tracked individuals were less than three minutes long (Fig. 3). On average $50.9 \pm 10.2\%$ of flights were less than one minute long (Table 4). The longest recorded flight was 12 minutes. Flight durations were not evenly distributed across the night ($\chi^2 = 39.94$, $d.f. = 12$, $P \leq 0.001$ — Fig. 3) with longer flights in the first (18:00) and last hour (06:00) of the night. Bats also

spent a larger proportion of their time flying early in the night ($\chi^2 = 50.21$ $d.f. = 12$, $P \leq 0.001$ — Fig. 4). On the nights when we were able to track bats for full nights (12.5 hrs), the six bats had an average cumulative flight time of 68.6 minutes \pm 29.7 minutes (SD). Thus, when bats were away from the roost they spent a small proportion of their time in flight (ca 11%) versus hanging, perched.

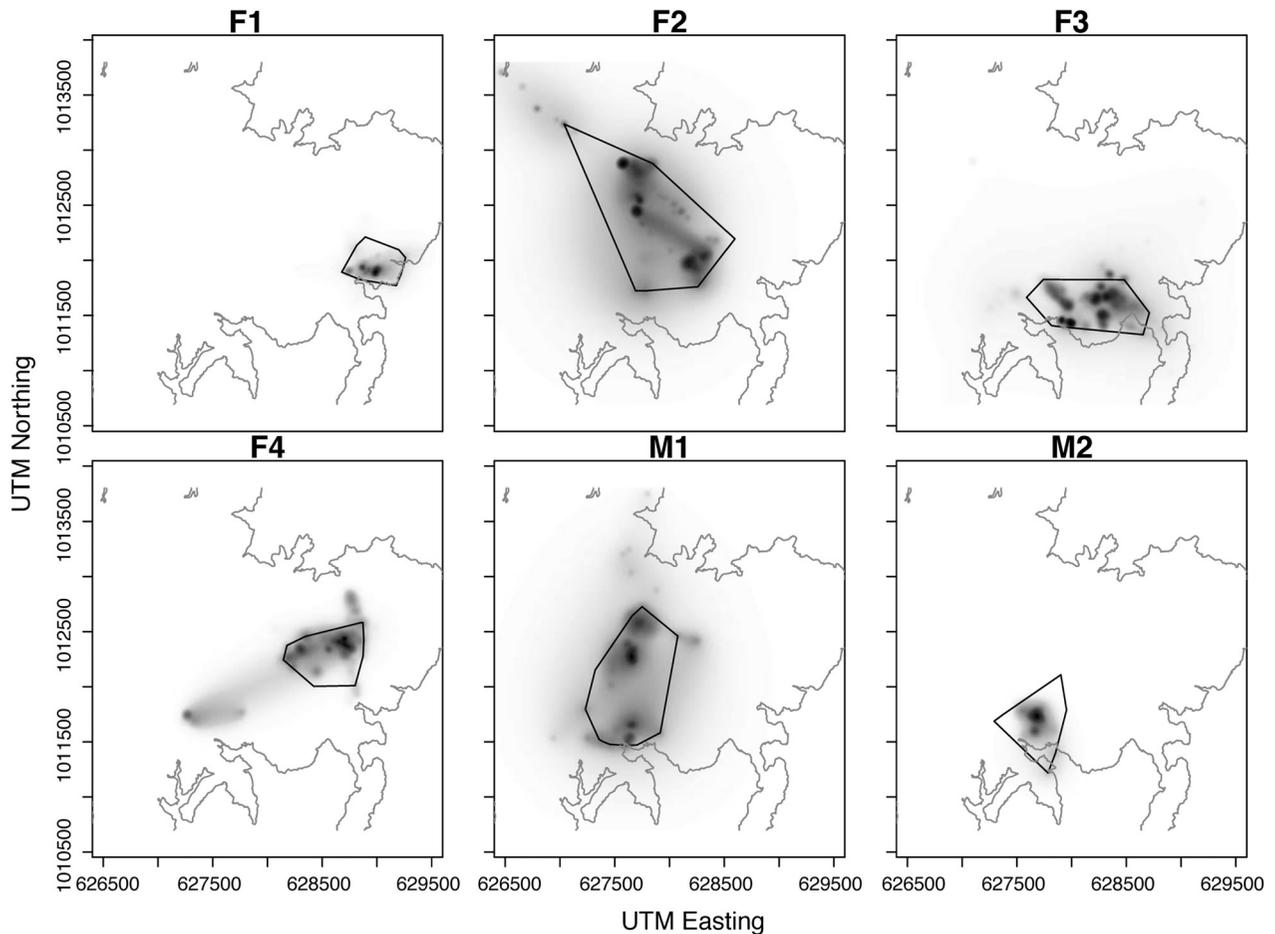


FIG. 2. Utilization distributions for individual bats from dynamic Brownian bridge models. Utilization increases with increased saturation from white (no use) to black (high use). Polygons indicate the 95% MCP for each bat and the outline of BCI is given for reference

TABLE 4. Activity patterns for radiotracked bats of *T. cirrhosus* in Barro Colorado Island. Sunset was at 18:29 for the full length of the tracking period; sunrise ranged from 5:59 to 6:28

Bat	Emergence time (range)	Return time (range)	% flights <1 min	% flights >1 min	Average cumulative minutes in flight (range, N)	Number of tracking positions flying or (roosting)
F1	18:34 (18:28–18:40)	5:51 (5:48–5:56)	33.5	66.5	71.5 ± 4.1 (68–76, 3)	15 (195)
F2	18:39 (18:33–18:59)	6:12 (5:55–6:33)	54.3	45.7	61 ± 53.4 (29–121.5, 3)	22 (102)
F3	18:44 (18:29–19:20)	5:54 (5:40–6:30)	54.6	45.4	66.2 ± 19.6 (43.5–78, 3)	14 (247)
F4	19:08 (19:05–19:11)	6:01 (5:56–6:06)	45.7	54.3	82 ± 55.9 (42.5, 121.5, 2)	20 (117)
M1	18:35 (18:24–18:45)	6:03 (6:00–6:07)	63.4	36.6	99 (1)	25 (87)
M2	18:53	6:02	53.1	46.9	56.5 ± 22.1 (32.5–76, 3)	61 (89)

DISCUSSION

Despite the small sample size, our results offer insights into the roosting, movement and activity patterns of *T. cirrhosus*, and highlight avenues for future study. As in Kalko *et al.* (1999), *T. cirrhosus* in the current study roosted in hollow cashew trees (*A. excelsum*), and as we hypothesized, showed low roost site fidelity via the frequent roost switching we observed, and high variation in length of day roost tenure (1 to 18 days). Brigham (1991) proposed that

bats show low roost site fidelity in tree roosts in contrast to high roost site fidelity in buildings and caves. This may be due to the inherent impermanence of vegetative roosts, or to their potentially greater accessibility to predators (Lewis, 1995). It would be interesting for future studies to examine whether *T. cirrhosus* that roost in human-made structures have higher roost site fidelity than tree-roosting individuals.

The small roosting groups and frequent roost switching for *T. cirrhosus* suggest the fission-fusion

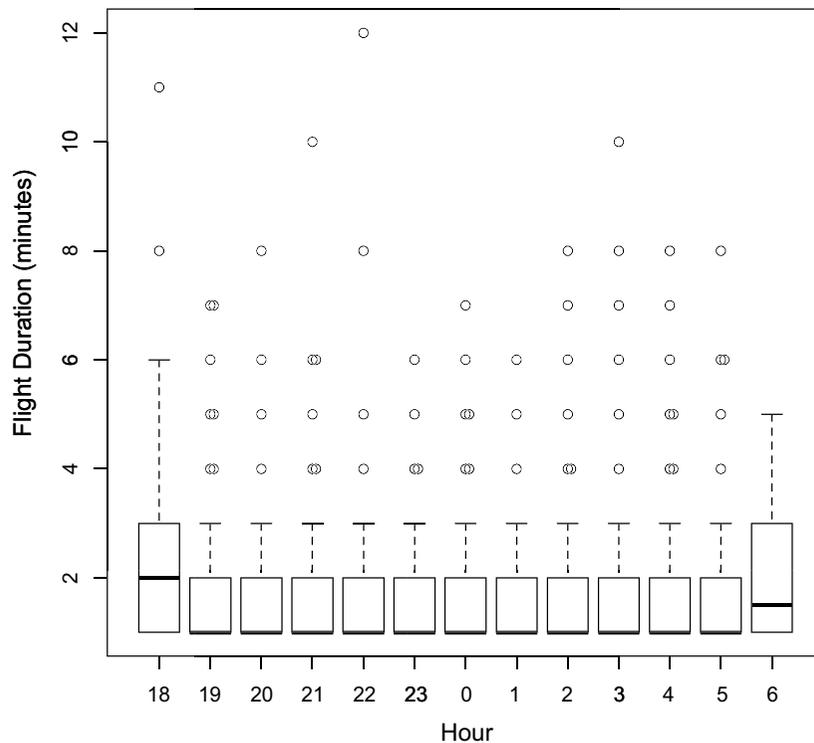


FIG. 3. Boxplot of duration of the flights of *T. cirrhosus* over the course of the night (18:00 to 6:00). Thick lines indicate the median flight durations, edges of the boxes indicate first and third quartiles, whiskers extend to 1.5 times the interquartile range, and circles are outliers

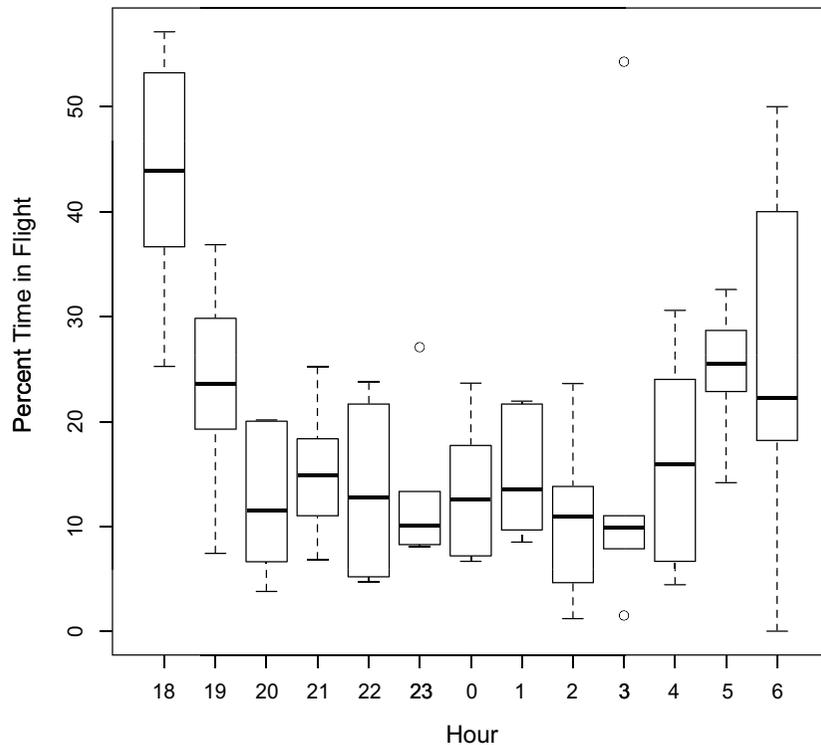


FIG. 4. Boxplot of percent of time *T. cirrhosus* spent in flight versus stationary (hanging) over the course of the night (18:00 to 6:00)

sociality, as has been demonstrated for many bat species (Patriquin and Ratcliffe, 2016). We found *T. cirrhosus* roosting in mixed-sex groups of three to five individuals. We also observed certain individuals switching roosts with the same individuals. These observations are consistent with the roosting patterns of other cavity-dwelling bat species, in which bats consistently roost with the same individuals even when frequently roost switching (Kerth and König, 1999; Rhodes, 2007). Social roosting in bats can provide a number of advantages, including thermoregulation (Zahn, 1999) and mating opportunities, but also access to social information (Ratcliffe and Hofstede, 2005; Dechmann, *et al.*, 2010; O'Mara *et al.*, 2014a; Gager *et al.*, 2016; Ramakers *et al.*, 2016). Roosting in a large group, however, can also increase the risk of disease transmission (Terborgh and Janson, 1986), and can attract predators (Fenton *et al.*, 1994). The fission-fusion dynamics exhibited by many bat species (e.g., Willis and Brigham, 2003; Popa-Lisseanu *et al.*, 2008; Fleischmann and Kerth, 2014; Patriquin *et al.*, 2016) may therefore be a compromise between the costs and benefits of social roosting (Kashima *et al.*, 2013).

Bats that live in temperate regions generally have large home ranges, often over 100 ha (Bonaccorso *et al.*, 2015) and up to 1,588 ha (Amelon *et al.*, 2014). Tropical forests are much denser habitats,

and tropical frugivorous and nectarivorous bat species that roost in small groups tend to have home ranges of less than 15 hectares (Albrecht *et al.*, 2007; Chaverri *et al.*, 2007; Rothenwöhler *et al.*, 2011), potentially due to the high density of fruits and flowers in these habitats (Bonaccorso *et al.*, 2005). In contrast, we report large home ranges for *T. cirrhosus* of 60 ha (using 95% MCP), larger than 100% MCP areas for other sympatric bat species for which there is radiotracking data (Albrecht *et al.*, 2007; Chaverri *et al.*, 2007; Rothenwöhler *et al.*, 2011).

The sensory ecology of some tropical bat species may allow them to take advantage of the density of food in Neotropical forests, and forage in a small area. For example, *Micronycteris microtis* has very small foraging areas, but is a generalist hunter feeding primarily on insects and small vertebrates (Santana *et al.*, 2011), and has the ability to locate stationary and silent prey that are undetectable for other bat species (Geipel *et al.*, 2013). This foraging behaviour may enable *M. microtis* to access more prey per area than many other predatory bats. In contrast, we speculate that *T. cirrhosus*'s sensory strategy of hunting by eavesdropping on prey mating calls may enable it to locate prey at greater distances, thereby generating larger foraging areas compared to other Neotropical bats. Low frequency

sound, such as frog calls, transmits further through forest than high frequency sound such as echolocation (Wily and Richards, 1978; Richards and Wiley, 1980). This should allow *T. cirrhosus* (or other bat species using a similar foraging strategy) to locate prey at much greater distances by using prey mating calls than by echolocation, potentially resulting in larger foraging areas than have been reported for bats that rely predominantly on echolocation to locate prey. To test this hypothesis would require comparisons of foraging areas between multiple pairs of closely related bat species that differ in prey localization behaviour. This may not be possible, and therefore this hypothesis remains speculative. Alternative explanations for the large home ranges and foraging areas of *T. cirrhosus* could include limitations in prey availability, or the relatively large body size of this bat species.

The bats in our study left their day roosts at dusk and did not return until dawn. The vast majority of flights made by bats were less than three minutes long, and the longest flight recorded was 12 minutes. Bats therefore spent only 11% of their night away from the roost in flight, with the majority of time spent hanging. We saw no evidence, however, of use of consistent night roosts. This supports the data from Kalko *et al.* (1999) which indicated that *T. cirrhosus* is a perch-hunting species, in contrast to aerial insectivores (Murray and Kurta, 2004) or nectarivores (Rothenwöhrer *et al.*, 2011) that exhibit longer flight times. The *T. cirrhosus* tracked in this study were likely capturing single prey items, hanging from a perch to eat them, then resting and sallying forth to capture another prey item or move to another location.

Kalko *et al.* (1999) observed continuous flight early in the night for *T. cirrhosus* and proposed that bats were foraging for frogs early and then for insects the rest of the night. We did see longer flight durations early in the night compared to the rest of the night and more time in flight early in the night with another increase approaching dawn (see Figs. 3 and 4). Túngara frogs (*Engystomops pustulosus*), one of the prey of *T. cirrhosus* (Tuttle and Ryan, 1985), start calling at dusk, peak in calling activity at around 21:00, and generally ceases before 00:30 (Ryan, 1983). It is possible that the increase in flight activity we saw early in the evening was bats hunting calling frogs, but this is not supported by either the low bat activity at 21:00 when frog calls should have been peaking, or the similar increase in activity we observed before dawn. Intriguingly, katydid calling behaviour has been shown to peak at dusk and

dawn, and this has been proposed as an explanation for the high activity levels of *Lophostoma silvicolum* activity at dusk and dawn on BCI (Lang *et al.*, 2006). *Trachops cirrhosus* is known to hunt katydids by eavesdropping on their calls, and it is possible that the increase in flight we saw at dusk and dawn was a product of bats hunting katydids. Further investigation is needed to understand the foraging strategies of this bat species across the night. Given the roosting and foraging locations that we found in this study, the high activity we saw from *T. cirrhosus* at dusk and again at dawn were most likely due to bats commuting to and from foraging areas and the roost.

In *T. cirrhosus* it has been hypothesized that one way bats may learn novel acoustic prey cues is by observing the foraging behaviour of knowledgeable conspecifics (Page and Ryan, 2006; Jones *et al.*, 2013). The use of social information in foraging has been demonstrated for multiple bat species including *Phyllostomus hastatus*, in which females use social calls to coordinate foraging (Wilkinson and Wenrick Boughman, 1998). Although on average we had minimal overlap in foraging areas, some of our radio tracked individuals overlapped up to 23.7% (M1 and F2), and evidence from automated proximity sensing technology demonstrates that *T. cirrhosus* associate at foraging sites (Ripperger *et al.*, 2016), reinforcing this potential for social learning (Page and Ryan, 2006; Jones *et al.*, 2013). Interestingly, our co-roosting females exhibited no overlap in foraging areas, hinting that there may be active spatial partitioning of foraging areas in co-roosting bats. Access to and use of social information by *T. cirrhosus* in the field is an area in particular need of further research.

As our knowledge of this species develops through research on prey perception and cognition in the laboratory it will continue to be informed by natural history. This study highlights the need for future research on social interactions and foraging behaviour in the field. Genetic data on relatedness combined with long-term monitoring of roosting and social interactions will provide important insights into the social structure of this species and how information is acquired and transmitted in a predator that learns fast both individually and socially, and has long-term memory for prey cues. As methods for tracking individuals improve with technological advancements in small GPS loggers, microphones, and cameras, we hope to see many advances in understanding what prey bats are capturing, the sensory strategies they are using for prey

capture, the specific individuals they are interacting with, and how their foraging behaviour changes over development, seasons, and years.

ACKNOWLEDGEMENTS

This manuscript is dedicated in loving memory of Eli Kalko. We are grateful to Hans-Ulrich Schnitzler for his help in sponsoring this research. The data were collected on BCI by Frank Hämsch with the help of Melva Olmos and Deborah Faria. We are grateful to the Smithsonian Tropical Research Institute for their long support of research on this species and to Anne Scharf for her advice on building Brownian bridges. We thank Brock Fenton, Gloriana Chaverri, and three anonymous reviewers for their helpful feedback.

LITERATURE CITED

- AKRE, K. L., and M. J. RYAN. 2010. Complexity increases working memory for mating signals. *Current Biology*, 20: 502–505.
- ALBRECHT, L., C. F. J. MEYER, and E. K. V. KALKO. 2007. Differential mobility in two small phyllostomid bats, *Artibeus watsoni* and *Micronycteris microtis*, in a fragmented neotropical landscape. *Acta Theriologica*, 52: 141–149.
- ALDRIDGE, H. D. J. N., and R. M. BRIGHAM. 1988. Load carrying and maneuverability in an insectivorous bat: a test of the 5% “rule” of radio-telemetry. *Journal of Mammalogy*, 69: 379–382.
- AMELON, S. K., F. R. THOMPSON, and J. J. MILLSPAUGH. 2014. Resource utilization by foraging eastern red bats (*Lasiurus borealis*) in the Ozark Region of Missouri. *Journal of Wildlife Management*, 78: 483–493.
- BATES, D., M. MAECHLER, B. BOLKER, and S. WALKER. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67: 1–48.
- BONACCORSO, F. J., J. R. WINKELMANN, and D. G. P. BYRNES. 2005. Home range, territoriality, and flight time budgets in the black-bellied fruit bat, *Melonycteris melanops* (Pteropodidae). *Journal of Mammalogy*, 86: 931–936.
- BONACCORSO, F. J., C. M. TODD, A. C. MILES, and P. M. GORRESEN. 2015. Foraging range movements of the endangered Hawaiian hoary bat, *Lasiurus cinereus semotus* (Chiroptera: Vespertilionidae). *Journal of Mammalogy*, 96: 64–71.
- BONATO, V., K. G. FACURE, and W. UIEDA. 2004. Food habits of bats of subfamily Vampyrinae in Brazil. *Journal of Mammalogy*, 85: 708–713.
- BRIGHAM, R. M. 1991. Flexibility in foraging and roosting behaviour by the big brown bat (*Eptesicus fuscus*). *Canadian Journal of Zoology*, 69: 117–121.
- CALENGE, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modeling*, 197: 516–519.
- CHAVERRI, G., O. E. QUIRÓS, and T. H. KUNZ. 2007. Ecological correlates of range size in the tent-making bat *Artibeus watsoni*. *Journal of Mammalogy*, 88: 477–486.
- CLARE, E. L., B. K. LIM, M. B. FENTON, and P. D. N. HEBERT. 2011. Neotropical bats: estimating species diversity with DNA barcodes. *PLoS ONE*, 6: e22648.
- CRAMER, M. J., M. R. WILLIG, and C. JONES. 2001. *Trachops cirrhosus*. *Mammalian Species*, 656: 1–6.
- DECHMANN, D. K. N., B. KRANSTAUBER, D. GIBBS, and M. WIKELSKI. 2010. Group hunting—a reason for sociality in molossid bats? *PLoS ONE*, 5: e9012.
- FENTON, M. B., I. L. RAUTENBACH, S. E. SMITH, C. M. SWANPOEL, J. GROSELL, and J. VAN JAARSVELD. 1994. Raptors and bats: threats and opportunities. *Animal Behaviour*, 48: 9–18.
- FLEISCHMANN, D., and G. KERTH. 2014. Roosting behavior and group decision making in 2 syntopic bat species with fission-fusion societies. *Behavioral Ecology*, 25: 1240–1247.
- GAGER, Y., O. GIMENEZ, M. T. O’MARA, and D. K. N. DECHMANN. 2016. Group size, survival and surprisingly short lifespan in socially foraging bats. *BMC Ecology*, 16: 2.
- GEIPEL, I., K. JUNG, and E. K. V. KALKO. 2013. Perception of silent and motionless prey on vegetation by echolocation in the gleaning bat *Micronycteris microtis*. *Proceedings of the Royal Society*, 280B: 20122830.
- GIANNINI, N. P., and E. K. V. KALKO. 2004. Trophic structure in a large assemblage of phyllostomid bats in Panama. *Oikos*, 105: 209–220.
- HALFWERK, W., M. M. DIXON, K. J. OTTENS, R. C. TAYLOR, M. J. RYAN, R. A. PAGE, and P. L. JONES. 2014a. Risks of multimodal signaling: bat predators attend to dynamic motion in frog sexual displays. *Journal of Experimental Biology*, 217: 3038–3044.
- HALFWERK, W., P. L. JONES, R. C. TAYLOR, M. J. RYAN, and R. A. PAGE. 2014b. Risky ripples allow bats and frogs to eavesdrop on a multisensory sexual display. *Science*, 343: 413–416.
- HUIJMAN, R. J. 2016. geosphere: spherical trigonometry. R package version 1.5-5. Available at <https://CRAN.R-project.org/>.
- HORNE, J. S., E. O. GARTON, S. M. KRONE, and J. S. LEWIS. 2007. Analyzing animal movements using Brownian bridges. *Ecology*, 88: 2354–2363.
- JONES, P. L., M. J. RYAN, V. FLORES, and R. A. PAGE. 2013. When to approach novel prey cues? Social learning strategies in frog-eating bats. *Proceedings of the Royal Society*, 280B: 20132330.
- KAHLE, D., and H. WICKHAM. 2013. ggmap: spatial visualization with ggplot2. *The R Journal*, 5: 144–161.
- KALKO, E. K. V., D. FRIEMEL, C. O. HANDLEY, JR., and H.-U. SCHNITZLER. 1999. Roosting and foraging behaviour of two Neotropical gleaning bats, *Tonatia silvicola* and *Trachops cirrhosus*. *Biotropica*, 31: 344–353.
- KASHIMA, K., H. OHTSUKI, and A. SATAKE. 2013. Fission-fusion bat behavior as a strategy for balancing the conflicting needs of maximizing information accuracy and minimizing infection risk. *Journal of Theoretical Biology*, 318: 101–109.
- KERTH, G., and B. KONIG. 1999. Fission, fusion and nonrandom associations in female Bechstein’s bats (*Myotis bechsteinii*). *Behaviour*, 136: 1187–1202.
- KRANSTAUBER, B., R. KAYS, S. D. LAPOIN, M. WIKELSKI, and K. SAFI. 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Animal Ecology*, 81: 738–746.
- LANG, A. B., E. K. V. KALKO, H. RÖMER, C. BOCKHOLDT, and D. K. N. DECHMANN. 2006. Activity levels of bats and katydids in relation to the lunar cycle. *Oecologia*, 146: 659–666.
- LEWIS, S. 1995. Roost fidelity of bats: a review. *Journal of Mammalogy*, 76: 481–496.
- MURRAY, S. W., and A. KURTA. 2004. Nocturnal activity of the endangered Indiana bat (*Myotis sodalis*). *Journal of Zoology (London)*, 262: 197–206.
- O’MARA, M. T., D. K. N. DECHMANN, and R. A. PAGE. 2014a.

- Frugivorous bats evaluate the quality of social information when choosing novel foods. *Behavioral Ecology*, 25: 1233–1239.
- O'MARA, M. T., M. WIKELSKI, and D. K. N. DECHMANN. 2014b. 50 years of bat tracking: device attachment and future directions. *Methods in Ecology and Evolution*, 5: 311–319.
- PAGE, R. A., and P. L. JONES. 2016. Overcoming sensory uncertainty: factors affecting foraging decisions in frog-eating bats. Pp. 285–312, in *Psychological mechanisms in animal communication* (M. A. BEE and C. T. MILLER, eds.). *Animal signals and communication 5*. Springer International Publishing, New York, 320 pp.
- PAGE, R. A., and M. J. RYAN. 2005. Flexibility in assessment of prey cues: frog-eating bats and frog calls. *Proceedings of the Royal Society of London*, 272B: 841–847.
- PAGE, R. A., and M. J. RYAN. 2006. Social transmission of novel foraging behavior in bats: frog calls and their referents. *Current Biology*, 16: 1201–1205.
- PATRIQUIN, K. J., M. L. LEONARD, H. G. BRODERS, W. M. FORD, E. R. BRITZKE, and A. SILVIS. 2016. Weather as a proximate explanation for fission-fusion dynamics in female northern long-eared bats. *Animal Behaviour*, 122: 47–57.
- PATRIQUIN, K. J., and J. M. RATCLIFFE. 2016. Should I stay or should I go? Fission-fusion dynamics in bats. Pp. 65–103, in *Sociality in bats* (J. ORTEGA, ed.). Springer International Publishing, Cham, 308 pp.
- POPA-LISSEANU, A.G., F. BONTADINA, O. MORA, and C. IBÁÑEZ. 2008. Highly structured fission-fusion societies in an aerial-hawking, carnivorous bat. *Animal Behaviour*, 75: 471–482.
- RAMAKERS, J. J. C., D. K. N. DECHMANN, R. A. PAGE, and M. T. O'MARA. 2016. Frugivorous bats prefer information from novel social partners. *Animal Behaviour*, 116: 83–87.
- RATCLIFFE, J., and H. TER HOFSTEDE. 2005. Roosts as information centres: social learning of food preferences in bats. *Biology Letters*, 1: 72–74.
- R CORE TEAM. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at <https://www.R-project.org/>.
- RHODES, M. 2007. Roost fidelity and fission-fusion dynamics of white-striped free-tailed bats (*Tadarida australis*). *Journal of Mammalogy*, 88: 1252–1260.
- RICHARDS, D. G., and R. H. WILEY. 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. *American Naturalist*, 115: 381–399.
- S. RIPPERGER, D. JOSIC, M. HIEROLD, A. KOELPIN, R. WEIGEL, M. HARTMANN, R. PAGE, and F. MAYER. 2016. Automated proximity sensing in small vertebrates: design of miniaturized sensor nodes and first field tests in bats. *Ecology and Evolution*, 6: 2179–2189.
- ROTHENWÖHRER, C., N. I. BECKER, and M. TSCHAPKA. 2011. Resource landscape and spatio-temporal activity patterns of a plant-visiting bat in a Costa Rican lowland rainforest. *Journal of Zoology*, 283: 108–116.
- RYAN, M. J. 1983. Sexual selection and communication in a neotropical frog, *Physalaemus pustulosus*. *Evolution*, 37: 261–272.
- RYAN, M. J., and M. TUTTLE. 1982. Bat predation and sexual advertisement in a neotropical anuran. *American Naturalist*, 119: 136–139.
- SANTANA, S. E., I. GEIPEL, E. R. DUMONT, M. B. KALKA, and E. K. V. KALKO. 2011. All you can eat: high performance capacity and plasticity in the common big-eared bat, *Micronycteris microtis* (Chiroptera: Phyllostomidae). *PLoS ONE* 6: e28584.
- TERBORGH, J., and C. H. JANSON. 1986. The socioecology of primate groups. *Annual Review of Ecology and Systematics*, 17: 111–135.
- TRILLO, P. A., K. A. ATHANAS, D. H. GOLDHILL, K. L. HOKE, and W. C. FUNK. 2012. The influence of geographic heterogeneity in predation pressure on sexual signal divergence in an Amazonian frog species complex. *Journal of Evolutionary Biology*, 26: 216–222.
- TROUSDALE, A. W., D. C. BECKETT, and S. L. HAMMOND, S. L. 2008. Short-term roost fidelity of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) varies with habitat. *Journal of Mammalogy*, 89: 477–484.
- TUTTLE, M., and M. J. RYAN. 1981. Bat predation and the evolution of frog vocalizations in the Neotropics. *Science*, 214: 677–678.
- WILEY, R. H., and D. G. RICHARDS. 1978. Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology*, 3: 69–94.
- WILKINSON, G., and J. WENRICK BOUGHMAN. 1998. Social calls coordinate foraging in greater spear-nosed bats. *Animal Behaviour*, 55: 337–350.
- WILLIS, C. K. R., and R. M. BRIGHAM. 2003. Roost switching, roost sharing and social cohesion: forest-dwelling big brown bats, *Eptesicus fuscus*, conform to the fission-fusion model. *Animal Behaviour*, 68: 495–505.
- ZAHN, A. 1999. Reproductive success, colony size and roost temperature in attic-dwelling bat *Myotis myotis*. *Journal of Zoology (London)*, 247: 275–280.

Received 22 March 2017, accepted 31 July 2017

Associate Editor: Burton Lim