

Ecological Correlates of Roost Fidelity in the Tent-Making Bat *Artibeus watsoni*

Gloriana Chaverri*†, Oscar E. Quirós†, Melquisedec Gamba-Rios‡ & Thomas H. Kunz*

* Center for Ecology and Conservation Biology, Department of Biology, Boston University, Boston, MA, USA

† Instituto de Estudios Tropicales, Golfito, Costa Rica

‡ Escuela de Biología, Universidad Latina de Costa Rica, San José, Costa Rica

Correspondence

Gloriana Chaverri, Center for Ecology and Conservation Biology, Department of Biology, Boston University, Boston, MA 02215, USA.
E-mail: gchaverri@upacificosur.org

Received: September 28, 2006

Initial Acceptance: January 8, 2007

Final Acceptance: January 8, 2007

(S. Forbes)

doi: 10.1111/j.1439-0310.2007.01365.x

Abstract

Roost switching is a common occurrence in bats, yet the causes and consequences of such behavior are poorly understood. In this study we explore the ecological correlates of roost fidelity in the tent-making bat *Artibeus watsoni*, particularly focusing on the effect of sex, reproductive status, and roost availability using a three-factor general linear model (GLM). We estimated roost fidelity of radio-tracked individuals and found that the GLM was significant ($R^2 = 0.72$, $F_{10,34} = 8.91$, $p < 0.001$). Significant interaction terms were observed for relative roost availability and sex ($F_{4,34} = 16.96$, $p < 0.001$), and relative roost availability and reproductive status ($F_{6,34} = 7.62$, $p < 0.001$), indicating that variation in roost fidelity among males and females, and among individuals under different breeding conditions, depended on relative roost availability at the site where they were radio-tracked. Individuals in areas of high roost availability exhibited lower roost fidelity than those sampled in areas of lower roost availability. Females exhibited less roost fidelity than males for all roost availability categories, but the difference between males and females was only significant at high roost availability. The general pattern of decreased roost fidelity as roost availability increased was also prevalent among individuals in different breeding conditions. Additionally, satellite males exhibited higher roost fidelity than resident males in areas of low roost availability, and lactating females had higher roost fidelity than non-breeding females in areas of medium roost availability. Our study thus demonstrates that sex, reproductive status, and roost availability all affect roost fidelity in the tent-making bat *A. watsoni*, and also suggests that roost availability is the most important factor influencing roost fidelity in this bat, providing the first quantitative evidence that roost fidelity is correlated with roost abundance in a single species.

Introduction

The roosting ecology of bats is often viewed as a complex interaction between physiological, behavioral, and morphological adaptations, and the events associated with roosting have probably played a major role in the evolution of these mammals

(Kunz 1982; Kunz & Lumsden 2003). Bats depend almost exclusively upon their roosts for facilitating social interactions, avoiding predators, promoting energy conservation, and for protection from inclement weather, and the roosting habits of bats are known to be influenced by the distribution and abundance of food, the diversity and abundance of

roosts, and the energetic tradeoffs between body size and the physical environment (Kunz & Lumsden 2003).

Movement between alternate roosts appears to be a common occurrence in many species of bats, and hence understanding how individuals move among roosting sites is important in identifying the costs and benefits of this behavior. Potential costs of switching roosts include increased time and energy required to locate potential roosts, exposure to predators while searching for roosts, and energetic costs of transporting young (Alcock 1989). In addition, moving between roosting sites may also increase the costs of finding and communicating with other group members (Lewis 1995). Roost switching, however, may help reduce parasite loads (Lewis 1995; Reckardt & Kerth 2005) or prevent detection of roost sites as reliable prey sources by predators (Fenton et al. 1994; Winkelmann et al. 2000). It may also decrease the energy spent commuting to foraging areas (Kunz 1982; Wilkinson 1985; Fleming 1988), and allow individuals to become familiar with alternate roosts in case the primary roost is destroyed or disturbed (Lewis 1995).

Some of the ecological factors known to influence roost switching in bats include the relative abundance and permanence of roosts, the proximity and stability of food resources, response to predator pressure, and human disturbance (Kunz 1982; Lewis 1995). Bats that occupy spatially abundant roosts, such as foliage or tree cavities, are more likely to change roosts frequently (e.g. Vonhof & Barclay 1996; Willis & Brigham 2004; Chaverri & Kunz 2006), whereas species using scarce resources such as caves may remain faithful to these sites for extremely long periods of time (e.g. McCracken & Bradbury 1981). Caves also provide permanent roosting sites because of their longevity, thus increasing fidelity to these sites (Lewis 1995). In contrast, species occupying less permanent structures, such as the developing leaves of plants, may experience extremely low roost fidelity (Findley & Wilson 1974; Happold & Happold 1996; Vonhof & Barclay 1996). These bats, however, often remain faithful to a clump of suitable roosting habitat (Happold & Happold 1996; Vonhof et al. 2004), probably because of the high availability of roosting resources. These abundant roosting resources, coupled with stable and abundant food resources, may further increase fidelity to particular roosting areas (Winkelmann et al. 2000; Chaverri et al. in press).

Roost fidelity is also known to change seasonally, and can be affected by reproductive condition, sex,

age, and social organization (Kunz 1982; Lewis 1995; Kunz & Lumsden 2003). For example, males have been observed to exhibit greater fidelity to roosts than females (e.g. Storz et al. 2000; Young 2001; Reckardt & Kerth 2006), although some studies have observed the opposite (e.g. Goiti et al. 2006; Gomes et al. 2006). Seasonal differences in roost fidelity have been observed in *Pteropus vampyrus*, where individuals exhibited two movement phases: one of continuous movement between roost sites, which coincided with late pregnancy and lactation, and the second where almost no movement occurred (Gumal 2004). In addition, fidelity may differ between adults and juveniles (Law 1993), but may not differ between adults and subadults (Menzel et al. 2001).

The numerous studies addressing roost fidelity in bats demonstrate not only how important this trait is for understanding more complex behavioral patterns, but also the ease with which roost fidelity can be measured in the field. However, few studies have gone beyond simple qualitative measures and explanations for why some individuals switch roosting sites often while others express high site fidelity within the same population. Thus, in the present study we use a multivariate approach to help understand the ecological correlates of roost switching behavior in the tent-making bat *Artibeus watsoni*, and do so by examining three factors known to affect roost fidelity in bats, namely sex, reproductive condition, and roost availability.

Artibeus watsoni is a small (approx. 11 g) phyllostomid bat that ranges from Veracruz, México through Central America to Colombia. It is usually found below elevations of 800 m, in semi-deciduous and evergreen lowland forests, second growth and fruit groves (Reid 1997). It feeds primarily on fruits and, to a lesser extent, insects and pollen (LaVal & Rodríguez-H 2002). This species roosts under modified leaves, and exploits a higher diversity of plant species than any other tent-making bat (Kunz & Lumsden 2003). Chaverri & Kunz (2006) found that in Corcovado National Park and in the Golfito Wildlife Refuge, both located in southwestern Costa Rica, *A. watsoni* roosts most commonly in *Carludovica palmata*, *Asplundia alata*, *Heliconia imbricata* and *Calathea lutea*, which are most likely modified into tents by males. Individuals from both study sites display not only different tent fidelity indices, but also use plant species in different proportions, most likely as a result of human activities and their effect on the local roosting resources (Chaverri & Kunz 2006).

Methods

Study sites

This study was conducted at two protected areas in southwestern Costa Rica from June 2003 to September 2004. The first study area, Corcovado National Park (8°28'N, 83°35'W) is a 42 468-ha park with altitudes ranging from sea level to 550 m. The Golfito Wildlife Refuge (8°38'N, 83°11'W), which is comprised of 2810 ha, has altitudes ranging from sea level to 505 m. Within Corcovado, we sampled populations from six different sites, all located near the Sirena Research Station. Three of these sites, Mirador de Orero (MO), Danta Primario (DP), and Espavel (ES) were located mostly in undisturbed primary forests, and Guanacaste (GU), Naranjo 1 (NA1) and Naranjo 2 (NA2) were all located in secondary forests. GU is located near the coast, and differs from all other sites in that no females have ever been captured there. Thus, males that were captured at this site were classified as satellite.

Bats in Golfito were sampled from two plantations bordering areas that were deforested or in intermediate stages of regeneration. Primary forests with steep elevations up to 230 m surround these sites. The first two sites were located near the Playa Cacao sector, and one was located in a cacao plantation (CT) mixed with bananas and other exotic fruit-bearing trees, and the second from an area of early secondary growth (PC). The third site was located in an abandoned bamboo plantation (BO), which contains abundant pioneer understory plants.

Field data collection

We captured bats during the day at their roosts using hand nets mounted on telescoping poles (Kunz & Kurta 1988), and collected data on sex, age and reproductive status (Anthony 1988; Racey 1988). Each bat was fitted with an individually numbered plastic wing band (A.C. Hughes, Hampton Hill, Middlesex, UK), with females banded on the left wing and males banded on the right wing. We attached radiotransmitters (model BD-2 and BD-2N; Holohil Systems Ltd, Woodlawn, ON, Canada; 0.47–0.51 g; 3.9–4.25% of the bat's body mass) using Skin Bond Cement (Smith and Nephew United, Largo, FL, USA) to a total of 45 bats. We used radioreceivers (TRX-1000S; Wildlife Materials, Inc., Carbondale, IL, USA) with three-element Yagi antennae to locate bats during the day.

During radio-tracking, we approached potential roosts carefully and verified the presence of bats fitted with radiotransmitters using binoculars. Each occupied tent was approached cautiously to record the identity of bats occupying the roost, and a numbered tag was placed on vegetation near the tent, but not on it, to avoid disturbing the roosting bats. We then recorded tent location using a Global Positioning System (eTrex; Garmin International Inc., Olathe, KS, USA). Bats were located daily in their tent roosts as long as the radiotransmitter remained active and attached to the bats (5–17 d).

To record roost switching behavior, we calculated an index of roost fidelity for all radiotagged bats. We recorded whether individuals remained in the same tent the day after initial observation, if they moved to a previously unoccupied tent, or if they changed roosts but returned to a tent previously occupied by this same individual. Roost fidelity (RF) was quantified using the Chaverri & Kunz (2006) index:

$$RF = \frac{2(STAY) + 1(RETURN) - 1(MOVE)}{STAY + RETURN + MOVE},$$

where RF is a measure of roost fidelity of a single bat, STAY the number of days a bat stayed in a single roost, RETURN the number of days the bat returned to previously used tents, and MOVE the number of times the bat was found in a different tent than the previous day, divided by the total number of observations. This index ranks a bat to a higher fidelity level when it uses a tent on consecutive days than when the same tent is used intermittently for the same number of days. Roost fidelity assumes values of -1 (complete infidelity) to 2 (complete fidelity). Because bats always moved to a different roost after being captured the first time, we excluded this initial movement from our analyses of roost fidelity.

Statistical analyses

To determine the effect of three ecological correlates on roost fidelity (RF), we used a nonorthogonal, three-factor weighted general linear model (GLM) (Timm & Mieczkowski 1997), with RF as the dependent variable, and sex, reproductive status, and relative roost availability as categorical independent variables. Independent variables were divided into the following categories: sex (male, female); reproductive status (satellite male, resident male, pregnant female, lactating female, and non-reproductive female); relative roost availability (low, medium, high). Males were classified as either resident or

satellite if captured in areas where females were present (resident) or absent (satellite). Females were classified as pregnant if the lower abdomen was distended and/or a foetus could be detected by palpation (Racey 1988), and classified as lactating if the nipples were enlarged and milk could be expressed. If tests of within-subject effects for the GLM were significant, Tukey's pairwise comparison at $\alpha = 0.05$ was used to identify differences within factors. If we found significant interactions between factors, we performed pairwise comparisons between all categorical combinations of the interacting factors using an independent-samples t-test, and compared only categories for which sample sizes were >2 .

Relative roost availability was determined by calculating the residual of the linear regression with relative population abundance as the independent variable, and roost abundance as the dependent variable, thus providing a measure of the relative number of tents available per bat. Estimates of relative roost availability for all sites were then transformed into three categories using SPSS (SPSS Inc., Chicago, IL, USA). SPSS converts continuous numeric data to a discrete number of categories by creating new variables containing the categorical data. Data were categorized based on percentile groups, with each group containing approximately the same number of cases. For example, a specification of three groups, as in our study, would assign a value of 1 to cases below the 33rd percentile, 2 to cases between the 33rd and 66th percentile, and 3 to cases above the 66th percentile.

Relative roost abundance for a given site was estimated based on the number of tents used by all simultaneously radio-tagged individuals at that site. Although this assessment of roost abundance may underestimate actual availability of roosts per unit area, we decided to use this variable because occupied and unoccupied tents were more often found in areas that we classified as having high roost availability, and vice versa, demonstrating that our estimate was relatively accurate.

Relative population abundance was calculated as the number of bats captured per net hour, based on one 12×2 m mist net opened for 1 h. While estimating relative population abundance using mist nets may be problematical because the ability to capture individuals may be influenced by weather, habitat, time of day, experience, and net location (MacArthur & MacArthur 1974; Karr 1981, 1990), this method is relatively free of observer bias, and allows sampling to be standardized. In addition, the validity of this classification system for relative abundance

estimates in our study was supported by roost survey data, because areas classified as having high relative abundance had a high rate of encounters with roosting bats, whereas in low relative abundance areas, encounter rates were correspondingly low.

Results

During the 16-mo research period, we obtained data on roost fidelity for 45 bats ($n = 14$ males, 31 females) that were radio-tracked for an average of 9.98 d (± 2.30 , range = 5–17). More than half of individuals (62.3%, 28/40) were from Corcovado, whereas 37.7% (17/45) were from Golfito. Thirty-nine percent (12/31) of females were lactating, 22% (7/31) were pregnant, whereas 39% (12/31) appeared to be reproductively inactive. We also radio-tracked 11 adult resident males and three adult satellite males, and individuals were sampled mostly in areas of medium relative roost availability (42.2%, 19/45), whereas 31.2% of bats were sampled in areas of high roost availability (14/45) and 26.6 from areas of low roost availability (12/45). Mean roost fidelity observed was 0.99 (± 0.82), although some individuals showed either complete infidelity (RF = -1.00) or complete fidelity (RF = 2.00) to their tents during the radio-tracking period.

The univariate model of between-subject effects in the General Linear Model was significant ($R^2 = 0.72$, $F_{10,34} = 8.91$, $p < 0.001$), indicating that sex, reproductive status, and relative roost availability were all significantly correlated with roost fidelity. Significant interaction terms were observed for relative roost availability and sex ($F_{4,34} = 16.96$, $p < 0.001$), and relative roost availability and reproductive status ($F_{6,34} = 7.62$, $p < 0.001$), indicating that variation in roost fidelity among males and females, and among individuals in different breeding conditions, was explained by relative roost availability at the site where they were radio-tracked.

Pairwise comparisons between all categorical combinations of the interacting factors show that both males and females in areas of high roost availability exhibited significantly lower roost fidelity than males and females in areas of low and medium roost availability (Table 1; Fig. 1), but the difference in roost fidelity was not significant between areas of low and medium roost availability. Females had lower average roost fidelity than males at all roost availability categories, but the difference between males and females in low and medium roost availability was not significant (Table 1), while the difference was significant at high roost availability. In addition, the

Table 1: Results of the independent-sample t-test comparing males and females in areas of low, medium (Med), and high roost availability

Categories	df	t	p
Male-Low, Male-Med	7	0.11	0.91
Male-Low, Male-High	8	3.05	0.01
Male-Med, Male-High	7	3.63	0.008
Female-Low, Female-Med	20	0.29	0.77
Female-Low, Female-High	14	5.51	<0.001
Female-Med, Female-High	22	5.73	<0.001
Male-Low, Female-Low	10	0.66	0.52
Male-Med, Female-Med	17	1.02	0.31
Male-High, Female-High	12	2.95	0.01

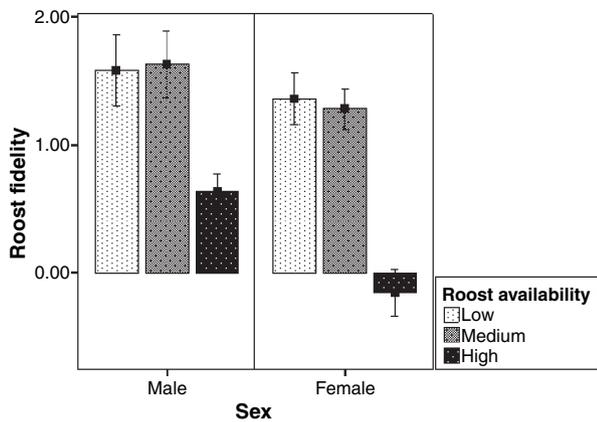


Fig. 1: Mean roost fidelity for males and females sampled in areas of low, medium and high roost availability. Error bars show mean \pm 1.0 standard error, and vertical lines separate sex categories

difference in average roost fidelity between males and females increased as roost availability increased (Fig. 1).

The general pattern of decreased roost fidelity as roost availability increased was also prevalent among individuals in different breeding conditions (Fig. 2). For example, resident males in areas of medium roost availability exhibited significantly higher roost fidelity than resident males sampled in areas with high roost availability, and pregnant females in areas of low roost availability exhibited significantly higher roost fidelity than females in areas of high roost availability (Table 2). Moreover, roost fidelity in non-breeding females decreased significantly from areas of medium to high roost availability. Satellite males exhibited significantly higher roost fidelity than resident males in areas of low roost availability, and lactating females had significantly higher roost fidelity than non-breeding females in areas of medium roost availability. Comparisons of roost fidelity between many reproductive categories in areas with

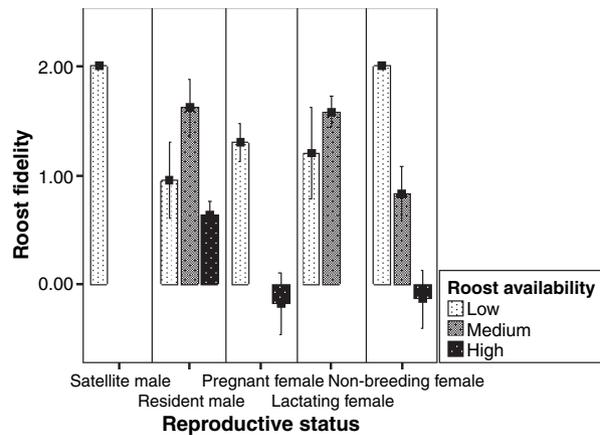


Fig. 2: Mean roost fidelity for satellite and resident males, and for pregnant, lactating and non-breeding females sampled in areas of low, medium and high roost availability. Error bars show mean \pm 1.0 standard error, and vertical lines separate reproductive categories

Table 2: Results of the independent-sample t-test comparing satellite and resident males, and pregnant, lactating, and non-breeding females (NBF) in areas of low, medium (Med), and high roost availability

Categories	df	t	p
Resident-Low, Resident-Med	4	1.52	0.20
Resident-Low, Resident-High	5	1.09	0.32
Resident-Med, Resident-High	7	3.63	0.008
Pregnant-Low, Pregnant-High	5	4.03	0.01
Lactating-Low, Lactating-Med	10	1.14	0.28
NBF-Med, NBF-High	9	2.63	0.02
Pregnant-Low, Lactating-Low	3	4.02	0.03
Satellite-Low, Resident-Low	4	0.22	0.83
Lactating-Med, NBF-Med	13	2.83	0.01
Pregnant-High, NBF-High	7	0.10	0.92

similar roost availability did not yield significant differences (Table 2), and small sample sizes did not allow comparisons between many categories (see Fig. 2).

Discussion

Our study strongly suggests that roost availability was the most important factor correlating with roost fidelity in *A. watsoni* because roost fidelity among all sex classes and reproductive conditions decreased as roost availability increased. This suggests that roost availability may be the most important factor facilitating roost switching behavior in *A. watsoni*, and that other factors, such as sex and reproductive status, may only correlate with roost switching to the degree that roosts are available for promoting such

behavior. Similarly, roost abundance seems to play an important role in the roosting ecology of other bat species. For example, Brigham (1989) observed that the big brown bat, *Eptesicus fuscus*, exhibited low roost fidelity in areas where individuals roosted in tree cavities, whereas bats sampled in human-made structures exhibited higher roost fidelity. These differences, according to Brigham, are likely to be the result of the availability of roosts, as human-made structures are more limited than natural cavity roosts (in his study area), and thus bats roosting in the former are more site-faithful. Intra-specific differences in roost fidelity have also been observed in the fruit-eating bat *Artibeus jamaicensis*. Morrison (1979) observed that individuals in tree cavities were more site faithful than those using foliage roosts, which is likely the result of the greater abundance of foliage compared to cavities in trees. Additional data on roost fidelity in other species suggest that those using abundant roosting resources, such as foliage, tend to be less site-faithful than those species using scarcer roosting sites such as buildings or caves (Lewis 1995). However, comparisons between populations of the same species inhabiting different habitats may hold the best prospects for testing the postulated link between roost abundance and roost fidelity in bats, given that populations tend to differ less than do species, reducing the confounding effects of covarying traits on the analysis (Lott 1991; Arnold 1992). Our study thus provides the first quantitative evidence that roost fidelity is correlated with roost abundance in a single species.

Roost fidelity decreased as roost availability increased in *A. watsoni* probably as a result of a significant decline in the cost–benefit ratio associated with roost switching. At low roost availability, moving between scarce roosts was probably too costly because of an increase in the time and energy locating roosts and from the exposure to predators while searching for them (Alcock 1989). However, the more abundant roosting resources at some sites may have promoted roost switching as a means of preventing detection of roost sites as reliable prey sources by predators (Fenton et al. 1994; Winkelmann et al. 2000), and as a means to decrease the energy spent commuting to distant foraging areas (Kunz 1982; Wilkinson 1985; Fleming 1988). Roost switching may have also helped reduce parasite loads (Lewis 1995; Reckardt & Kerth 2005), which may explain why species with low roost fidelity usually exhibit lower parasite loads (ter Hofstede & Fenton 2005).

Our study also shows that in areas of high roost availability, males exhibited greater roost fidelity than females. Sex is known as an important factor influencing roost fidelity in bats, and males of several species, such as *Desmodus rotundus*, *Balionycteris maculata*, and *Cynopterus sphinx* are more faithful to their roosts than females (Wilkinson 1985; Storz et al. 2000; Hodgkison et al. 2003). The increased fidelity to roosts that we observed in male *A. watsoni* may allow competing resident males to defend a resource that is costly to construct and that may provide a means of attracting potential mates (Kunz & McCracken 1996). The fact that male *A. watsoni* remained faithful to particular roosting sites more often than females, despite the high female turnover, suggests that territorial defense of tent-roosts or roosting areas by males may occur in this species. Territorial defense of roosts or roosting sites has often been observed in many other bats as well (e.g. Bradbury & Vehrencamp 1976; Morrison 1979; Kunz et al. 1983; Williams 1986; Fleming 1988; Kunz & McCracken 1996; Storz et al. 2000; Dechmann et al. 2005), and access to females is thought to be linked to such defensive strategies. However, the fact that differences between males and females were not significant in areas of lower roost availability supports the notion that roost switching is too costly for females when roosts are scarce, but that the cost–benefit ratio decreases as roosts increase.

We found no differences in roost fidelity between females in different breeding conditions, except for lactating and non-breeding females in areas of medium roost availability. Lactating females expressed high roost fidelity in our study most likely because during the night they relocate their non-volant pups often, and thus may accrue high energetic costs if these pups are moved among many tents. In addition, lactating females may remain faithful to particular tents as a means to secure stable social interactions with other group members. Securing social interactions with other lactating females may increase survival of pups, as they spend less energy in thermoregulation while their mothers are foraging (Trune & Slobodchikoff 1978). Females may also benefit from the presence of other individuals because they may help guard their pup (O'Farrell & Studier 1973), or, in some species, even engage in communal nursing (Wilkinson 1988, 1992).

In conclusion, our study demonstrates that sex, reproductive status, and roost availability all significantly correlate with roost fidelity in the tent-making bat *A. watsoni*. However, we have shown that these variables must not be analyzed independently from

one another, because their interaction was as important in shaping roost-switching behavior as was the independent influence of each variable. Our results also suggest that relative roost availability is the most important factor correlating with roost fidelity in this bat, and many behavioral differences between males and females, and between individuals in different breeding conditions, were only perceivable when roosts were readily available. Our study thus provides the first quantitative evidence that roost fidelity is correlated with roost abundance in a single species, allowing us to further identify the costs and benefits of roost switching behavior in bats.

Acknowledgements

We thank M. Sagot, G. Solano, J. Calderón, S. Alvarado, A.S. Turmelle, N. Estrada, O. Berrocal and Y. López for field assistance. We also thank J. Guevara and W. Barrantes for research permits, and the Corcovado National Park rangers and staff for providing accommodation, field assistance and valuable advice. This study was funded by grants to GC from Idea Wild, Consejo Nacional de Ciencia y Tecnología and Ministerio de Ciencia y Tecnología, American Society of Mammalogists, Cleveland Metroparks Zoo, Bat Conservation International, Conservation, Food and Health Foundation, Inc., and Boston University's Center for Ecology and Conservation Biology. All research protocols used in this study were approved by Boston University's Animal Care and Use Committee.

Literature Cited

- Alcock, J. 1989: Animal Behavior. Sinauer, Sunderland, MA.
- Anthony, E. L. P. 1998: Age determination in bats. In: Ecological and Behavioral Methods for the Study of Bats. (Kunz, T. H., ed.). Smithsonian Institution Press, Washington, DC, pp. 47–58.
- Arnold, S. J. 1992: Behavioral variation in natural populations. VI. Prey responses by two species of garter snakes in three regions of sympatry. *Anim. Behav.* **44**, 705–719.
- Bradbury, J. W. & Vehrencamp, S. L. 1976: Social organization and foraging in emballonurid bats. I. Field studies. *Behav. Ecol. Sociobiol.* **1**, 337–381.
- Brigham, R. M. 1989: Flexibility in foraging and roosting behaviour by the big brown bat (*Eptesicus fuscus*). *Can. J. Zool.* **69**, 117–121.
- Chaverri, G. & Kunz, T. H. 2006: Roosting ecology of the tent-roosting bat *Artibeus watsoni* (Chiroptera: Phyllostomidae) in southwestern Costa Rica. *Biotropica*. **38**, 77–84.
- Chaverri, G., Quirós, O. E. & Kunz, T. H. in press: Ecological correlates of range size in the tent-making bat *Artibeus watsoni*. *J. Mammal* in press.
- Dechmann, D. K. N., Kalko, E. K. V., König, B. & Kerth, G. 2005: Mating system of a Neotropical roost-making bat: the white-throated, round-eared bat, *Lophostoma silviculum* (Chiroptera: Phyllostomidae). *Behav. Ecol. Sociobiol.* **58**, 316–325.
- Fenton, M. B., Rautenbach, I. L., Smith, S. E., Swane-poel, C. M., Grosell, J. & van Jaarsveld, J. 1994: Raptors and bats: threats and opportunities. *Anim. Behav.* **48**, 9–18.
- Findley, J. S. & Wilson, D. E. 1974: Observations on the neotropical disk-winged bat, *Thyroptera tricolor* Spix. *J. Mammal.* **55**, 562–571.
- Fleming, T. H. 1988: The Short-tailed Fruit Bat. Univ. of Chicago Press, Chicago, IL.
- Goiti, U., Aihartza, J. R., Almenar, D., Salsamendi, E. & Garin, I. 2006: Seasonal foraging by *Rhinolophus euryale* (Rhinolophidae) in an Atlantic rural landscape in northern Iberian Peninsula. *Acta Chiropt.* **8**, 141–155.
- Gomes, M. N., Uieda, W. & Latorre, M. D. D. D. 2006: Influence of sex differences in the same colony for chemical control of vampire *Desmodus rotundus* (Phyllostomidae) populations in the state of Sao Paulo, Brazil. *Pesqui. Vet. Bras.* **26**, 38–43.
- Gumal, M. T. 2004: Diurnal home range and roosting trees of a maternity colony of *Pteropus vampyrus natunae* (Chiroptera: Pteropodidae) in Sedilu, Sarawak. *J. Trop. Ecol.* **20**, 247–258.
- Happold, D. C. D. & Happold, M. 1996: The social organization and population dynamics of leaf-roosting banana bats, *Pipistrellus nanus* (Chiroptera, Vespertilionidae), in Malawi, east-central Africa. *Mammalia*. **60**, 517–544.
- Hodgkison, R., Balding, S. T., Akbar, Z. & Kunz, T. H. 2003: Roosting ecology and social organization of the spotted-winged fruit bat, *Balionycteris maculata* (Chiroptera: Pteropodidae), in a Malaysian lowland dipterocarp forest. *J. Trop. Ecol.* **19**, 667–676.
- ter Hofstede, H. M. & Fenton, M. B. 2005: Relationships between roost preferences, ectoparasite density, and grooming behaviour of neotropical bats. *J. Zool. (Lond.)*. **266**, 333–340.
- Karr, J. R. 1981: Surveying birds with mist nets. In: Estimating Numbers of Terrestrial Birds, Vol. 6 (Ralph, C. J. & Scott, J. M., eds). Studies in Avian Biology, Cooper Ornithological Society, Lawrence, Kansas. pp. 62–67.
- Karr, J. R. 1990: The avifauna of Barro Colorado Island and the Pipeline Road, Panama. In: Four Neotropical Forests (Gentry, A. H., ed.). Yale Univ. Press, New Haven, CT, pp. 183–198.

- Kunz, T. H. 1982: Roosting ecology of bats. In: Ecology of Bats (Kunz, T. H., ed.). Plenum Press, New York, pp. 1—50.
- Kunz, T. H. & Kurta, A. 1988: Capture methods and holding devices. In: Ecological and Behavioral Methods for the Study of Bats (Kunz, T. H., ed.). Smithsonian Institution Press, Washington, DC, pp. 1—29.
- Kunz, T. H. & Lumsden, L. F. 2003: Ecology of cavity and foliage roosting bats. In: Bat Ecology (Kunz, T. H. & Fenton, M. B., eds). Univ. of Chicago Press, Chicago, IL, pp. 3—87.
- Kunz, T. H. & McCracken, G. F. 1996: Tents and harems: apparent defense of foliage roosts by tent-making bats. *J. Trop. Ecol.* **12**, 121—137.
- Kunz, T. H., August, P. V. & Burnett, C. D. 1983: Harem social organization in cave roosting *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Biotropica* **15**, 133—138.
- LaVal, R. K. & Rodríguez-H, B. 2002: Murciélagos de Costa Rica. Instituto Nacional de Biodiversidad, Heredia (Costa Rica).
- Law, B. S. 1993: Roosting and foraging ecology of the Queensland blossom bat (*Syconycteris australis*) in north-eastern New-South-Wales – flexibility in response to seasonal-variation. *Wildl. Res.* **20**, 419—431.
- Lewis, S. E. 1995: Roost fidelity of bats: a review. *J. Mammal.* **76**, 481—496.
- Lott, D. F. 1991: Intraspecific Variation in the Social Systems of Wild Vertebrates. Cambridge Univ. Press, Cambridge.
- MacArthur, R. H. & MacArthur, A. T. 1974: On the use of mist nets for population studies of birds. *Proc. Natl Acad. Sci. USA* **71**, 3230—3233.
- McCracken, G. F. & Bradbury, J. W. 1981: Social organization and kinship in the polygynous bat *Phyllostomus hastatus*. *Behav. Ecol. Sociobiol.* **8**, 11—34.
- Menzel, M. A., Carter, T. C., Ford, W. M. & Chapman, B. R. 2001: Tree-roost characteristics of subadult and female adult evening bats (*Nycticeius humeralis*) in the Upper Coastal Plain of South Carolina. *Am. Midl. Nat.* **145**, 112—119.
- Morrison, D. W. 1979: Apparent male defense of tree hollows in the fruit bat, *Artibeus jamaicensis*. *J. Mammal.* **60**, 11—15.
- O'Farrell, M. J. & Studier, E. H. 1973: Reproduction, growth, and development in *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae). *Ecology* **54**, 18—30.
- Racey, P. A. 1988: Reproductive assessment in bats. In: Ecological and Behavioral Methods for the Study of Bats (Kunz, T. H., ed.). Smithsonian Institution Press, Washington, DC, pp. 31—45.
- Reckardt, K. & Kerth, G. 2005: The reproductive success of the parasitic bat fly *Basilia nana* (Diptera: Nycteribidae) is affected by the low roost fidelity of its host, the Bechstein's bat (*Myotis bechsteini*). *Parasitol. Res.* **98**, 237—243.
- Reckardt, K. & Kerth, G. 2006: The reproductive success of the parasitic bat fly *Basilia nana* (Diptera: Nycteribidae) is affected by the low roost fidelity of its host, the Bechstein's bat (*Myotis bechsteini*). *Parasitol. Res.* **98**, 237—243.
- Reid, F. A. 1997: A Field Guide to the Mammals of Central America and Southeast Mexico. Oxford Univ. Press, New York.
- Storz, J. F., Balasingh, J., Nathan, P. T., Emmanuel, K. & Kunz, T. H. 2000: Dispersion and site fidelity in a tent-roosting population of the short-nosed fruit bat (*Cynopterus sphinx*) in southern India. *J. Trop. Ecol.* **16**, 117—131.
- Timm, N. H. & Mieczkowski, T. A. 1997: Univariate and Multivariate General Linear Models: Theory and Applications Using SAS® Software. SAS Institute Inc., Cary, NC.
- Trune, D. R. & Slobodchikoff, C. N. 1978: Position of immatures in pallid bat clusters: a case of reciprocal altruism. *J. Mammal.* **58**, 469—478.
- Vonhof, M. J. & Barclay, R. M. R. 1996: Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia. *Can. J. Zool.* **74**, 1797—1805.
- Vonhof, M. J., Whitehead, H. & Fenton, M. B. 2004: Analysis of Spix's disc-winged bat association patterns and roosting home ranges reveal a novel social structure among bats. *Anim. Behav.* **68**, 507—521.
- Wilkinson, G. S. 1985: The social organization of the common vampire bat. I. Pattern and cause of association. *Behav. Ecol. Sociobiol.* **17**, 111—121.
- Wilkinson, G. S. 1988: Reciprocal altruism in bats and other mammals. *Ethol. Sociobiol.* **9**, 85—100.
- Wilkinson, G. S. 1992: Communal nursing in the evening bat, *Nycticeius humeralis*. *Behav. Ecol. Sociobiol.* **31**, 225—235.
- Williams, C. F. 1986: Social organization of the bat *Carollia perspicillata* (Chiroptera: Phyllostomidae). *Ethology* **71**, 265—282.
- Willis, C. K. R. & Brigham, R. M. 2004: Roost switching, roost sharing and social cohesion: forest-dwelling big brown bats, *Eptesicus fuscus*, conform to the fission-fusion model. *Anim. Behav.* **68**, 495—505.
- Winkelman, J. R., Bonaccorso, F. J. & Strickler, T. L. 2000: Home range of the southern blossom bat, *Syconycteris australis*, in Papua New Guinea. *J. Mammal.* **81**, 408—414.
- Young, R. A. 2001: The eastern horseshoe bat, *Rhinolophus megaphyllus*, in south-east Queensland, Australia: colony demography and dynamics, activity levels, seasonal weight changes, and capture-recapture analyses. *Wildl. Res.* **28**, 425—434.