ECOLOGICAL CORRELATES OF RANGE SIZE IN THE TENT-MAKING BAT *ARTIBEUS WATSONI*

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We examined variation in foraging- and roosting-range size in the tent-making bat *Artibeus watsoni*. We radiotracked 42 individuals at 2 sites in the Golfito Wildlife Refuge and 6 sites at Corcovado National Park, southwestern Costa Rica. Average home-range size of *A. watsoni* was the smallest recorded for a bat species (3.6 ha). Site, age, reproductive status, habitat, and season all had significant effects on foraging ranges, but sex and population abundance did not. Bats from the most productive sites, such as primary forests, had smaller foraging ranges, and subadults ranged farther than adults. During the dry season, females in late pregnancy had the smallest foraging ranges of all, most likely as a result of flight constraints imposed by the large fetus and an increase in fruit availability. Conversely, lactating females sampled during the early rainy season had among the largest foraging ranges. Males had significantly smaller roosting ranges than females, and adult bats sampled from areas of low roost abundance and high population abundance had smaller roosting ranges. However, subadults appeared to be unaffected by such changes in resource abundance, perhaps because they often roost in unmodified leaves. Although differences in resource availability and competition were important in determining roosting-range size, these effects were concealed by effects of reproductive activities such as mating, pregnancy, and lactation. Reproductive condition, along with foraging and roosting resource abundance, were largely responsible for determining ranging patterns in *A. watsoni*, but factors influenced foraging- and roosting-range size in different ways.

Key words: *Artibeus watsoni*, Costa Rica, foraging range, home range, roosting range

Home range is the area within the available habitat where an organism concentrates its daily activities, such as foraging, mating, and rearing young (Feldhamer et al. 2004). Understanding how ecological factors influence home-range size within and between species has important implications for the conservation of organisms and the habitats on which they depend. For example, annual home ranges of highly endangered or keystone species must be considered in designing the shape and size of protected areas (Caro 1998). In addition, information regarding range size of individuals may increase our knowledge of the vulnerability of a species to habitat degradation or to direct exploitation. For example, a species in which individuals use small home ranges may be especially susceptible to overexploitation because that species can be

extremely slow at recolonizing depleted areas (Vincent and Sadovy 1988). Similarly, species with particularly large ranges may be susceptible to extinction because individuals use widely dispersed, rare food items (Harcourt 1998), and thus may be the 1st to disappear if habitat fragmentation occurs because individuals may not be able to meet their daily energy requirements.

The size of the home range is known to depend upon many factors, such as body size and metabolic rate of the organism (Kelt and Van Vuren 1999; Swihart et al. 1988), and the quality of the resources available to an animal within the portion of habitat utilized (Kelt and Van Vuren 2001). Individuals with higher energetic needs, such as lactating females, or independent subadults that need more nutrients to grow yet lack food-gathering skills, are more likely to require larger home ranges (Clutton-Brock et al. 1982; Lindstedt et al. 1986). Males may also have large home ranges to increase the likelihood of breeding successfully (Lindstedt et al. 1986). The most intensively used area within the animal's home range is the core area, which may contain essential resources such as nests

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and water sources (Burt 1943). As with home range, core areas may differ seasonally, between sexes, in relation to habitat components, and also may vary as a result of reproductive status (Clutton-Brock et al. 1982).

In this study we present estimates of foraging-, roosting-, and home-range (combined range of foraging plus roosting) areas for the tent-making bat *Artibeus watsoni*, and explore intraspecific variation in range size. Based on a multivariate model, we suggest potential ecological factors that shape these differences, particularly focusing on the effect of site, sex, age, reproductive status, habitat, season, and relative population abundance. A multivariate model was chosen for this study because home-range size may be influenced by diverse metabolic, ecological, and behavioral attributes and their interactions (Kelt and Van Vuren 1999, 2001; Lindstedt et al. 1986). Thus, understanding what influences spacing behavior in free-ranging mammals requires knowledge of all potentially significant variables.

Artibeus watsoni is a small (approximately 11-g) phyllostomid bat that ranges from Veracruz, México, through Central America to Colombia. It is usually found below 800 m elevation, in semideciduous and evergreen lowland forests, 2nd growth, and fruit groves (Reid 1997). It feeds primarily on fruits, although to a lesser extent may consume insects and pollen (LaVal and Rodríguez-H. 2002). This species roosts under modified leaves, and is known to use more plant species for roosting than any other tent-making bat (Kunz and Lumsden 2003). In Corcovado National Park and in the Golfito Wildlife Refuge, both located in southwestern Costa Rica, *A. watsoni* prefers to roost in plants such as *Carludovica palmata*, *Asplundia alata*, *Heliconia imbricata*, and *Calathea lutea*, which appear to be modified into tents by males (Chaverri and Kunz 2006a). These males, and the accompanying females, exhibit divergent tent fidelity and plant preferences among study sites, most likely as a result of human activities and their effect on the local roosting resources (Chaverri and Kunz 2006a).

MATERIALS AND METHODS

Study sites and species identification.—This study was conducted in Corcovado National Park and Golfito Wildlife Refuge, both located in southwestern Costa Rica, from June 2003 through September 2004. Corcovado (8°28′N, 83°35′W) comprises 42,468 ha, with elevations ranging from sea level to 550 m, and Golfito (8°38′N, 83°11′W) comprises 2,810 ha, with elevations that range from sea level to 505 m. Within Corcovado, we sampled populations located at 6 different sites, all located near the Sirena Research Station. Two of these sites, Mirador de Orero (MO) and Danta Primario (DP), were located in undisturbed primary forests, and Espavel (ES) was located mostly in primary forest, although late secondary forests were found adjacent to this site. Guanacaste (GU), Naranjo 1 (NA1), and Naranjo 2 (NA2) were all located in secondary forests, although GU was located near the coast and differed from all other sites in that no females have ever been captured there, and thus it only contained satellite males.

Bats in Golfito were sampled from 2 plantations bordering areas that were either completely modified by humans or in intermediate stages of regeneration. Primary forests with steep elevations of up to 230 m also surrounded these plantations. The 1st site was located near the Playa Cacao sector (CT), in a cacao plantation mixed with bananas and other exotic fruit-bearing trees. The 2nd site was located in an abandoned bamboo plantation (BO), which contained abundant pioneer understory plants.

We identified bats based on the characteristics proposed by Timm and LaVal (1998) and Timm et al. (1999). We distinguished *A. watsoni* from the very similar *Artibeus phaeotis* based on the presence of a 3rd lower molar in the former, which is frequently observed in approximately 85% of the individuals (Timm and LaVal 1998). This small molar also was present in more or less 80% of our study animals, and most bats that did not have a 3rd lower molar were later identified also as *A. watsoni* because they were observed roosting with individuals that had the molar.

Field data collection.—We captured bats during the day at their roosts using hand nets with extendable poles (Kunz and Kurta 1988). Before attaching radiotransmitters, we recorded measurements such as length of forearm and body mass, and subsequently collected data on sex, age, and reproductive status. Each bat was fitted with an individually numbered, plastic wing band (A. C. Hughes, Hampton Hill, Middlesex, United Kingdom). We attached radiotransmitters (0.47–0.51 g; 3.9–4.25% of the bat's body mass; models BD-2 and BD-2N; Holohil Systems Ltd., Woodlawn, Ontario, Canada) using Skin Bond adhesive (Smith and Nephew United, Largo, Florida), and used 2 radioreceivers (TRX-1000S; Wildlife Materials Inc., Carbondale, Illinois) with 3-element Yagi antennae to locate bats during the day and night. We followed guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998) for the capture, handling, and care of mammals, and all protocols were approved by the Animal Care and Use Committee at Boston University.

To locate bats during the day we approached potential roosts carefully, and verified the presence of bats fitted with radiotransmitters using binoculars. We marked tents with flagging tape and individually numbered tags, and recorded data on tent characteristics and location using a global positioning system (eTrex; Garmin International Inc., Olathe, Kansas). Bats were located in their roosts as long as the radiotransmitter remained active and attached to the bats (5–17 days).

We obtained location fixes at night using the 2 radioreceivers positioned at distances of approximately 50 m. We recorded bearings as soon as the radiotagged bats started their nightly activities (about 1800 h), and obtained fixes approximately every 5 min at peak activity time. This interval was enough for the bats to traverse their entire home range, although after peak activity bats stayed longer at the same location, thus we recorded data as soon as we noted considerable movement (i.e., the bat was flying or the resulting bearings were >15° apart from the 1 last recorded). We collected data on foraging range until >50 fixes were obtained or for as long as the radiotransmitter remained active and attached to the bat. The

accuracy of our triangulation system was tested by calculating the distance between the estimated position of dummy transmitters to their actual location.

Signal location and range size analyses.—We used the software LOAS, version 3.0.1 (Ecological Software Solutions, Urnäsch, Switzerland), to estimate locations of bats during the night using the arithmetic mean estimator, and then used these fixes, along with data on roost location, to calculate foraging and roosting range using the Home Range Extension (Rogers and Carr 1998) in ARCVIEW software (Environmental Systems Research Institute, Redlands, California). Data points located at >300 m from the recording location were eliminated from the analysis because this distance represented the maximum range of reception for the radiotransmitters used.

We estimated the 100%, 95%, 85%, 75%, and 50% minimum convex polygons and fixed-kernel polygons for foraging range for bats with more that 29 fixes. The first 3 estimates were considered to account for total range size, whereas the latter 2 represent core area, or the most heavily used area within the individual's range. We did not include bats for which we had <29 locations in the analyses because kernel-based estimates from small samples are known to overestimate home-range size (Seaman and Powell 1996). We used only the 100% minimum convex polygons to estimate roosting ranges because of small sample sizes. We then merged roosting- and foraging-range coverages, and obtained the combined range (or home range) for all bats considered in the analysis. For the combined range we also estimated the 100%, 95%, 85%, 75%, and 50% minimum convex polygons and kernel polygons. We used all previous estimates of foraging and combined range size for 2 reasons: 1st, there is no consensus in the literature on which estimate may be most accurate, and the choice of which method is used seems to be based mostly on ease of comparison with other studies; and 2nd, we believe all these estimates to be equally important for understanding size of home range and core areas. Thus, we decided to keep all estimates and reduce them to a manageable, yet comprehensive data set.

Statistical analyses.—We assessed normality of range estimates based on the Kolmogorov–Smirnov test (Pardo-Igúzquiza and Dowd 2004). The Kolmogorov–Smirnov tests were significant, and thus roosting, foraging, and combined ranges were natural-log transformed to meet assumptions of normality. Independent variables used to test for variation in range size included site, sex, age, reproductive status, habitat, season, and relative population abundance. These variables were divided into the following categories: site (CT, BO, DP, ES, GU, MO, NA1, NA2), sex (male, female), age (juvenile, subadult, adult), reproductive status (nonreproductive male, active resident male, active satellite male, female in early stages of pregnancy, female in late stages of pregnancy, female that gave birth during the study, lactating female, postlactating female, nonreproductive female), habitat (plantation, secondary forest, primary forest), season (dry, early rainy, late rainy), and relative population abundance (low, medium, high).

Juveniles and subadults were distinguished from adults based on the presence of cartilaginous epiphyseal plates in metacarpals and phalanges (Anthony 1988), and juveniles were

further recognized from subadults if the former was still nursing and always roosting with its mother. Reproductive status was assessed in males by presence of descended testes (reproductively active—Racey 1988), and classified as either resident or satellite if captured in areas where females were present (resident) or absent (satellite). Females were classified as being in early pregnancy if a fetus was palpable but overall body mass of mother was <16.5 g, and in late pregnancy if weighing >16.5 g. Females that gave birth during the radiotracking period were classified as being in parturition, and females with enlarged nipples and from which milk could be expressed when mammary glands were palpated were classified as lactating. Postlactating females had enlarged nipples from which no milk could be expressed upon palpation. We classified the seasons as dry (December–March), early rainy (April–July), and late rainy (August–November).

Relative population abundance was calculated as the number of bats captured per net-hour; a net-hour equals one 12 × 2-m mist net opened for 1 h. Estimates of relative abundance for all sites were then transformed into 3 categories using SPSS, version 10 (SPSS Inc., Chicago, Illinois). Although estimating relative abundance using mist nets may be problematical because the capture of individuals may be influenced by weather, habitat, time of day, experience, and net location (Karr 1981, 1990; Kunz and Kurta 1988; MacArthur and MacArthur 1974), this method is relatively free of observer bias, and allows sampling to be standardized. The validity of this classification system for population abundance at our study sites is supported by roost survey data, because areas classified as having high relative population abundance had a high rate of encounters of roosting bats, whereas encounter rates were correspondingly low in areas with low relative abundance. However, we decided to minimize potential biases of our mistnetting sessions by assigning sites to broader categories instead of using the measurement data of bats per net hour.

The data set for natural log estimates of the 100%, 95%, 85%, 75%, and 50% minimum convex polygons and kernel polygons for foraging and combined range, as well as the natural-log 100% minimum convex polygon for roosting range, was reduced using the principal component analysis extraction method, with varimax rotation and Kaiser normalization (Jolliffe 2002). Eigenvalues > 1 were used to determine the number of components retained, and rotated scores were saved using the regression method in SPSS.

A nonorthogonal, 7-factor, weighted general linear model (Timm and Mieczkowski 1997) with the components generated by principal component analysis as the dependent variables, and site, sex, age, reproductive status, habitat, season, and relative population abundance as fixed factors, was used to determine the effect of all 7 independent variables on range size. If tests of within-subjects effects were significant, Tukey's pairwise comparison at alpha = 0.05 was used to identify differences within factors. If significant interaction terms were found, however, we did not perform the pairwise comparison because the effect of 1 factor is thus contingent upon other factor(s). SPSS, version 10, and SAS, version 8.1 (SAS Institute Inc., Cary, North Carolina) were used in all statistical

analyses, and values reported are means ± *SD*. Significance was assessed at an alpha of 0.05.

RESULTS

During the 16-month study period, we obtained >29 night radiofixes on 42 individuals, comprising 16 males and 26 females. The estimated precision of radiotracking data was ±36 m (*n* = 7). The number of fixes obtained per bat ranged between 30 and 92, with a mean of 53.5 ± 14.5 (Table 1). Bats were tracked for an average of 13.9 ± 4.5 h (range 3.5–21 h), and for 5.7 ± 1.1 days (range 4–8 days). Additionally, we were able to track all 42 bats to their day roosts for an average of 9.9 ± 2.5 days (range 4–16 days).

The average 100% minimum convex polygon for foraging range of all bats considered in the study was 3.0 ± 3.84 ha (range 0.01–23.8 ha). Bats used an average of 0.1 ± 0.11 ha of roosting range (range 0.003–0.5 ha), and the average 100% minimum convex polygon combined range (foraging range + roosting range, or home range) was 3.6 ± 4.06 ha (range 0.1–23.7 ha). The smallest foraging range recorded was that of an adult female that gave birth during the radiotracking period (0.01 ha), and the largest was recorded for a subadult male (23.7 ha). A female in late stages of pregnancy also had an extremely small foraging range (0.02 ha), and an adult male had a foraging range of 0.1 ha. The largest foraging range recorded for a female belonged to an adult nonbreeding individual tracked at the MO site (6.8 ha). The smallest roosting range was found in an adult satellite male (0.003 ha), and the largest in a subadult male (0.5 ha). The same adult satellite male that exhibited a very small roosting range of 0.003 ha also had the largest foraging range of all adult males (7.6 ha).

Data reduction.—The number of components retained during data reduction was 2. The 1st component had an eigenvalue of 10.5 and the 2nd component had an eigenvalue of 1.0. The variance explained by the 1st component after applying varimax rotation was 79.9%, and the 2nd component explained 8.9%. The 1st component, after varimax rotation, had loadings higher than 0.85 for the log-normal variables describing foraging range and combined range (100%, 95%, 85%, 75%, and 50% minimum convex polygons for foraging and combined range, and kernel for foraging and combined range), and the 2nd component loaded higher than 0.97 for the log-normal variable describing roosting range (100% minimum convex polygon for day range). Therefore, the 1st component of the principal component analysis (PC 1) included both foraging and combined range, and will subsequently be referred to as foraging range, and the 2nd component (PC 2) included only the roosting range.

General linear model for foraging range.—The univariate model of between-subjects effects was significant for PC 1, or foraging range ($R^2 = 0.87$, $F = 3.19$, *d.f.* = 28, 41, $P < 0.01$). Site, age, reproductive status, habitat, and season were all significantly correlated with foraging range, whereas neither sex nor relative population abundance had a significant effect on range size (Table 2). After Tukey's pairwise comparisons, we found that foraging range was significantly larger at site GU

TABLE 1.—Sample size for radiotracking data, including site, sex (male: M; female: F), and age (adult: A; subadult: SA; juvenile: J) for all individuals. Night data are divided in the total number of hours, days, and radiofixes obtained per individual. Roosting data represent the number of days we tracked bats to their day roosts. Site acronyms are defined in the ''Materials and Methods.''

Site	Bat no.	Sex	Age	Night (foraging)			Roosting (days)
				Hours	Days	Fixes	
CT	1392	M	A	13.5	4	70	13
	1437	F	A	17	6	61	13
	1666	F	A	13.5	4	58	12
	1687	F	A	13.5	4	63	8
	1744	F	A	17	6	61	11
	1745	M	A	16.5	6	61	11
	1761	F	A	10	5	50	8
	1892	M	SA	11.5	6	48	10
	1893	F	SA	10.5	5	44	6
	1895	M	J	11	6	50	11
BO	1973	F	A	8.5	4	48	13
	1976	F	A	8.5	4	47	9
	1977	M	A	8.5	4	47	10
DP	1698	M	A	9	7	57	11
	1699	M	A	5	5	47	7
	1700	F	A	7.5	7	57	14
	1701	F	A	3.5	4	34	4
	1702	F	A	6.5	7	56	9
	1704	F	A	13.5	6	58	7
	1706	F	A	9.5	7	57	12
ES	1487	F	A	12	6	80	5
	1488	M	A	13.5	7	92	10
	1489	F	A	13.5	7	90	8
GU	1251	M	A	20	6	29	10
	1470	M	A	20.5	7	32	13
	1881	M	A	20	6	30	11
	1918	M	SA	20.5	6	40	10
MO	1560	M	A	20.5	7	69	9
	1562	F	A	17	7	66	10
	1563	F	A	19	7	64	11
	1564	F	A	17.5	6	66	9
	1566	M	A	12.5	4	61	10
NA1	1621	F	A	17.5	5	50	9
	1641	M	A	17	5	50	7
	1783	F	A	21	6	61	11
	1784	F	A	17	5	50	9
	1786	F	A	17	5	50	8
	1787	M	A	16.5	5	50	12
NA2	1717	F	A	14.5	6	41	11
	2027	F	A	15	7	31	16
	2050	F	A	15.5	8	34	15
	2052	F	A	12.5	5	38	6
Average				13.90	5.71	53.52	9.98

compared to CT, BO, DP, and ES (Fig. 1a). Males and females did not differ significantly in foraging-range size (Fig. 1b), although subadults had significantly larger foraging ranges than adults (Fig. 1c). Reproductively active satellite males had significantly larger foraging ranges than active resident males, females in late pregnancy, and females in parturition. Nonreproductive males had larger foraging ranges than females at parturition and in late pregnancy, and females in late pregnancy had significantly smaller ranges than nonreproductive females (Fig. 1d). Bats in secondary forests had significantly larger

TABLE 2.—Summary of relevant statistics generated from the nonorthogonal, 7-factor general linear model. An asterisk (*) represents a significant interaction among the 2 terms specified.

Foraging range (PC 1)			Roosting range (PCA 2)		
Factor	F	P value	Factor	F	P value
Site	4.88	0.006	Sex	5.39	0.03
Sex	0.80	0.38	Age*site	7.16	0.01
Age	5.63	0.01	Age*habitat	6.18	0.02
Reproductive status	6.11	0.002	Age*relative abundance	11.04	0.005
Habitat	7.91	0.005	Reproductive status*site	2.70	0.04
Season	4.37	0.02	Reproductive status*season	3.72	0.03
Relative abundance	2.86	0.09	Reproductive status*relative abundance	3.72	0.01

foraging ranges than those in plantations or primary forests (Fig. 1e), and foraging ranges were smaller during the dry season than in the early rainy season (Fig. 1f). Population abundance had no significant effect on foraging-range size (Fig. 1g).

General linear model for roosting range.—The univariate model of between-subjects effects was significant for PC 2, or roosting range ($R^2 = 0.88$, $F = 3.46$, $d.f. = 28, 41$, $P = 0.01$). Sex had a significant effect on roosting range (Table 2), and males had significantly smaller roosting ranges than females. Significant interaction terms were observed between age and site, age and habitat, and age and relative population abundance. For example, adults in GU and NA1 had small roosting ranges compared to adults in BO and MO (Fig. 2a). The former sites were located in areas of secondary forests and of low relative population abundance, and the latter 2 were sampled from a plantation and a primary forest, both having high relative population abundance. Thus, adults in secondary forests

and in areas of low population abundance had smaller roosting ranges than adults in primary forests and in areas of higher population densities (Figs. 2b and 2c). However, roosting-range size was large in subadults regardless of the site, habitat, or relative abundance they were sampled in.

Significant interaction terms also were observed between reproductive status and site, reproductive status and season, and reproductive status and relative population abundance. For example, reproductively active males had very small roosting ranges in NA1 and CT, whereas they had larger roosting ranges in BO, ES, and MO (Fig. 2d). Females in parturition had very small roosting ranges in CT, whereas they had larger ranges in BO. In addition, roosting range in nonbreeding females was small in NA1, whereas it was very large in NA2. Active resident males had small roosting ranges during the dry season, but their range size increased during the late rainy season (Fig. 2e). Roosting-range size in pregnant females was small during the dry season, but increased in the
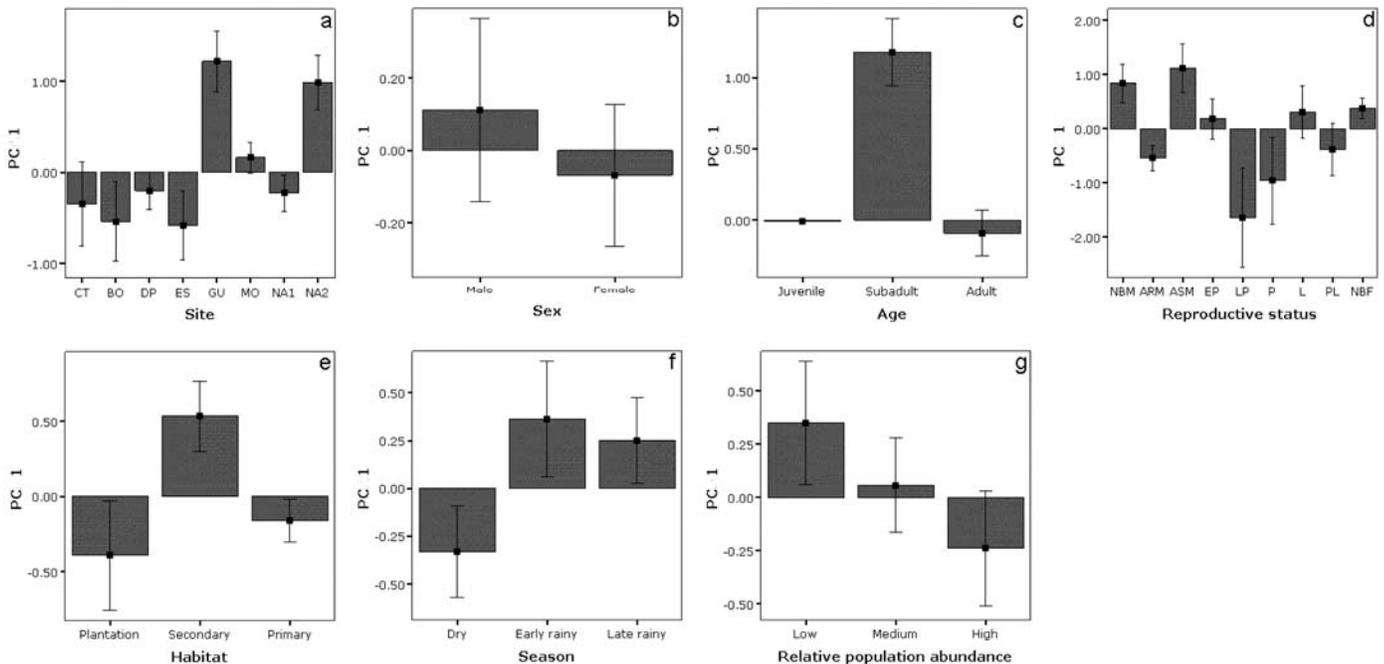

FIG. 1.—Mean foraging range (PC 1) for all 7 factors: a) site, b) sex, c) age, d) reproductive status (NRM: nonreproductive male, ARM: active resident male, ASM: active satellite male, EP: female in early pregnancy, LP: female in late pregnancy, P: parturition, L: lactating female, PL: postlactating female, NRF: nonreproductive female), e) habitat, f) season, g) relative population abundance. Error bars show mean ± 1.0 *SE*.
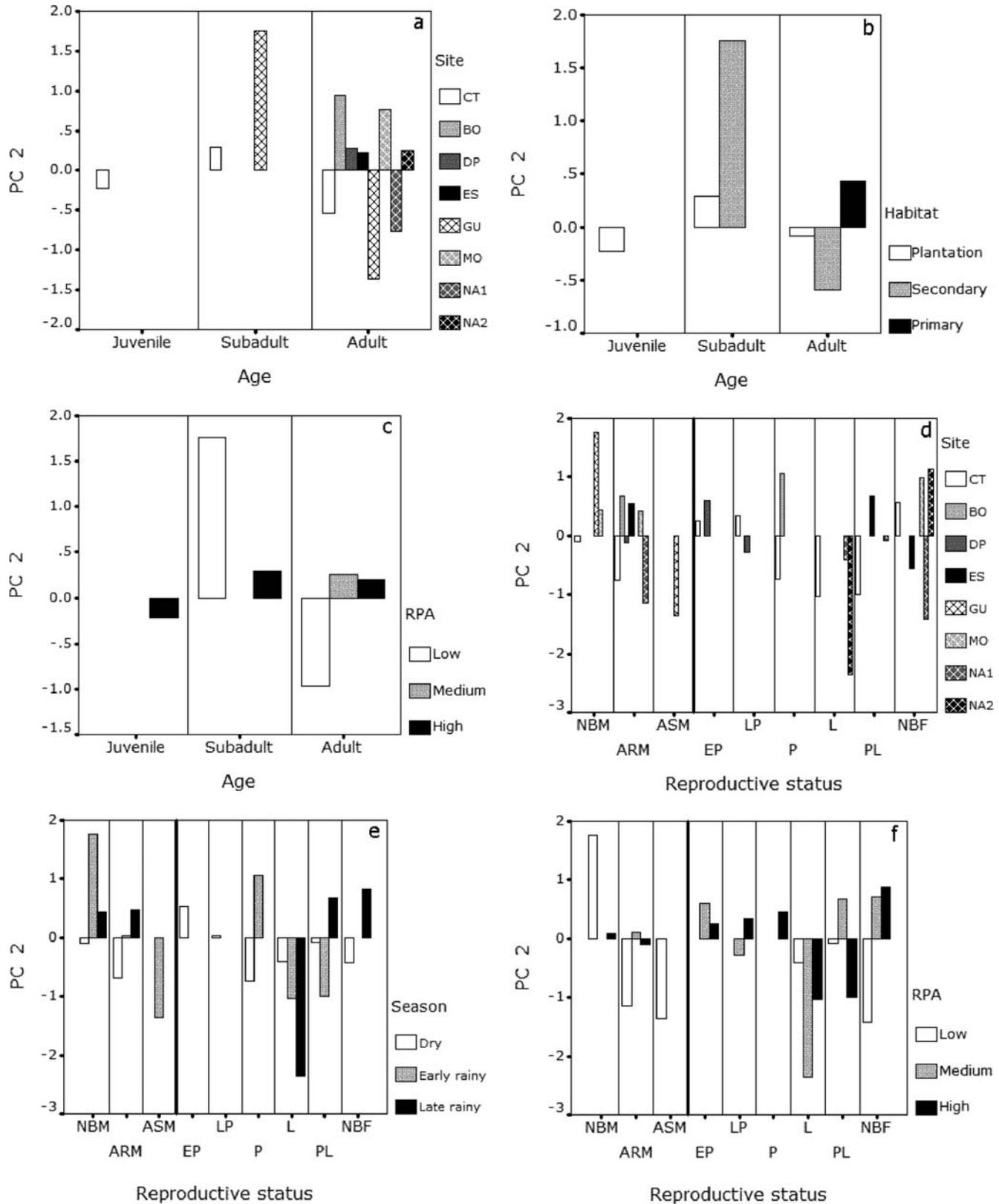
FIG. 2.—Mean roosting range (PC 2) for the interaction among age and a) site, b) habitat, and c) relative population abundance (RPA), and among reproductive status (NRM: nonreproductive male, ARM: active resident male, ASM: active satellite male, EP: female in early pregnancy, LP: female in late pregnancy, P: parturition, L: lactating female, PL: postlactating female, NRF: nonreproductive female) and d) site, e) season, f) and relative population abundance (RPA). Reference lines between categories are included, and a bold reference line between reproductive categories is used to distinguish between males and females.

early rainy season. However, roosting-range size decreased for lactating females from the dry to the late rainy season. Active resident males in areas of low population abundance had smaller roosting ranges than in areas of medium or high population abundance, and lactating females in areas of medium relative abundance had the smallest range compared to lactating females in low or high abundance (Fig. 2f). Finally, postlactating females in areas of high relative population abundance had the smallest roosting range compared to all other postlactating females.

DISCUSSION

Our results demonstrate that the small frugivorous bat *A. watsoni* has the smallest home range recorded for any bat species (3.6 ha). Other bats with relatively small ranges include the rain-forest bat species *Syconycteris australis*, *Macroglossus minimus*, and *Dobsonia minor* (5.1–5.8 ha—Bonaccorso et al. 2002; Winkelmann et al. 2000, 2003). These frugivorous and nectarivorous bats roost singly or in small groups, in diverse and widespread foliage or tree roosts, and their roosting ranges are usually contained within their foraging ranges. In contrast, insectivorous bats such as *Myotis lucifugus* and *Chalinolobus tuberculatus* roost in larger groups, and range over extensive areas of >17.6 ha (*M. lucifugus*—Henry et al. 2002) and 400 ha (*C. tuberculatus*—O'Donnell 2001). These differences in home-range size among bat species may be attributed to 2 important features of roosting and feeding resources: abundance and distribution. Thus, species such as *A. watsoni*, *S. australis*, *M. minimus*, and *D. minor* have small ranges most likely because of their relatively stable and abundant food sources and because of the high availability of roosting sites (Bonaccorso et al. 2002; Winkelmann et al. 2000).

Roosting range in *A. watsoni* was also very small compared to other bat species (0.1 ha). For example, *M. minimus* has a mean roosting range of 0.5 ha (Winkelmann et al. 2003) and *S. australis* is known to use roosting ranges of about 0.4 ha (Winkelmann et al. 2000). In contrast, *C. tuberculatus* has larger average roosting ranges of 9 ha (O'Donnell 2001). Interspecific variation in roosting range in bats is seldom addressed in the literature, although it may be attributed to the same factors influencing foraging ranges, namely resource distribution and abundance, especially regarding roost location and abundance with respect to food distribution. Within these parameters, roosting range may further be affected by roost permanence and the need for persistent roost switching. For example, bats using foliage roosts probably benefit from roost switching to minimize the ability of predators to locate them (Winkelmann et al. 2000). However, these roosts are often so abundant that the bat moves only short distances between roosting sites, particularly if their food is abundant and located near their day roosts. If roosts are ubiquitous but food is unpredictable in space and time, then the bats must relocate to patches of high food availability to minimize energy spent nightly while foraging, expanding their roosting ranges significantly. Although *A. watsoni* exhibits low roost fidelity (Chaverri and Kunz 2006a), its roosts and feeding resources are common and widely distributed, thus promoting the use of extremely small roosting ranges.

Ecological correlates of foraging-range size.—Our study strongly suggests that resource abundance was the most important determinant of foraging-range size in *A. watsoni*. Habitats in early successional stages are known to have fewer plant species than primary forests (Leigh 1999; Whitmore 1998), and potential feeding resources in the secondary forests sampled in our study were less abundant than in primary forests (G. Chaverri, pers. comm.). Therefore, bats in secondary forests had larger foraging ranges than bats sampled in primary forests because feeding resources were likely to be scarcer at the former sites. In addition, peak fruit availability in the tropics coincides with the end of the dry and the early rainy season (Janzen 1976; Leigh 1999). The reduction in foraging-range size during the dry season in our study thus suggests that food was more abundant at that time. This tendency for foraging-range size to decrease with increasing food availability has also been observed in other frugivorous bats, such as *Carollia perspicillata* (Charles-Dominique 1991; Fleming and Heithaus 1986), and in many other mammals (Fisher and Owens 2000; Herfindal et al. 2005; Larter and Gates 1994; Linders et al. 2004), demonstrating that an increasing degree of food availability is critical in determining ranging patterns.

Reproductive status of adult males also influenced foraging-range size in *A. watsoni*, and the large variation observed between resident and satellite males may be attributed to a mixed strategy of dominance and roaming (Gehrt and Fritzell 1999; Herfindal et al. 2005). In areas where female density is high, males adopt a dominance strategy to monopolize females by defending resources essential to them, such as roosts (Kunz and McCracken 1996), or by chasing intruding males (Bradbury and Vehrencamp 1976). Resident males thus remain closer to their roosting areas while foraging, as has been observed in other species of bats known to form harems such as *C. perspicillata*, *Artibeus jamaicensis*, and *Phyllostomus hastatus* (Fleming 1988; Kunz et al. 1998; Morrison and Morrison 1981). On the other hand, in areas of very low resource abundance, female density is probably low as well, and thus males adopt the roaming strategy, where they abandon dominance and secure access to females not by defending resources used by these females, but instead by visiting them in richer resource areas. Thus, the large night ranges of satellite males may be related to their search for mating opportunities, and not to their search for adequate foraging grounds.

Foraging-range size of females in *A. watsoni* appeared mainly determined by parenting duties, energetic demands, and movement constraints. Females with large energetic demands, no parenting duties, and no movement constraints, such as those in early pregnancy, had larger foraging ranges than females with higher movement constraints such as those in late pregnancy, where the fetus weighed approximately 30% of its mother's body mass (Chaverri and Kunz 2006b). During lactation, however, females traveled farther to acquire sufficient food to maintain both her and her pup's energetic demands (Kurta et al. 1989). Postlactating females did not seem to have

such high energetic demands, and thus reduced their foraging ranges relative to lactating females.

Age also seemed to be an important factor influencing foraging-range size in *A. watsoni*. Studies of foraging patterns in juvenile bats have found that newly volant individuals usually forage close to their roosts, probably as a result of poorly developed flight skills (Kunz 1974; O'Donnell 2001; Racey and Swift 1985), but that as these young individuals grow, they begin to range farther (Racey and Swift 1985), up to a point where they may be difficult to track (Winkelmann et al. 2003). We found that the only juvenile sampled had a small foraging and roosting range, and often remained inactive during the night, probably as a result of limited flight capabilities. On the other hand, all subadults tracked, male or female, had very large and unpredictable foraging and roosting ranges, probably because they disperse to other areas to establish territories as adults (Winkelmann et al. 2003), and because they require more nutrients to grow but have poorly developed foraging skills compared to adults.

Ecological correlates of roosting-range size.—The results of our study indicate that resource abundance was an important determinant of roosting-range size. However, foraging-range size decreased in areas of higher food abundance, whereas roosting-range size increased in areas of higher roost abundance. For example, adult bats surveyed in areas of lower roost abundance, such as plantations or secondary forests, or in areas of high relative population densities where tents must be shared among more bats, had smaller roosting ranges. This pattern suggests that adults increased their daily movements in response to increasing roost abundance, most likely to decrease the ability of predators to locate them, to decrease costs associated with commuting to more adequate foraging places, and to decrease parasitism (Eby 1991; Lewis 1995; Morrison 1979; Wilkinson 1985; Winkelmann et al. 2000). Nonetheless, subadults seemed unaffected by tent abundance, probably because they commonly roost under unmodified leaves (Chaverri and Kunz 2006a).

Our study also showed that sex influenced roosting-range size. Tents are a critical resource for *A. watsoni* because adults are known to roost exclusively in these structures (Chaverri and Kunz 2006a), and mating occurs frequently at these sites (Chaverri and Kunz 2006b). Thus, smaller ranges were probably the result of intense competition among neighboring males for roosting resources, and males with more, or better, roosts may have mating access to more females.

The interaction among reproductive condition and site, season, and relative population abundance demonstrates that although differences in resource abundance were important in determining roosting-range size in *A. watsoni*, their effect was concealed by the result of reproductive activities such as mating or lactation. For example, males had smaller roosting ranges during the mating season (dry and early rainy season— Chaverri and Kunz 2006b), most likely because they had to remain closer to their roosting sites to protect them against intruding males. However, in times of reproductive inactivity, such as during the late rainy season, roosting-range size increased because the costs of defending the roost exceeded the

benefits in terms of mating opportunities. Similarly, lactating females used small roosting ranges regardless of roost availability, most likely because they often relocate their nonvolant offspring among tents (Chaverri and Kunz 2006b). Using tents that were close together thus reduced the energetic cost of flying with their offspring.

In conclusion, we have shown that resource abundance, reproductive activities, and age were the primary factors determining ranging patterns in *A. watsoni*. However, our study showed that these variables must not be analyzed independently from one another, and the interaction among them was as important in shaping spatial movements as was the independent influence of each variable. Thus, multivariate approaches are the best way to address questions of intraspecific variability in home-range size, and the lessons provided by such analyses will help us understand the causes and consequences of space use in highly mobile organisms such as bats and their conservation implications. In addition, we observed that the same factors that affect foraging movements in *A. watsoni* had a completely different effect on roosting-range size. Roosts are probably as critical for bats as food (Kunz 1982; Kunz and Lumsden 2003), and the importance of these 2 resources has probably played a major role in the evolution of ranging patterns in these mammals. Thus, if we seek to understand what factors influence foraging and roosting behavior in bats, we should not only calculate and analyze these variables separately, but also explore alternate hypotheses to explain their variation.

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