



Range overlap and association patterns in the tent-making bat *Artibeus watsoni*

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Space use and ranging patterns of individuals have traditionally been used to identify social systems, and the amount of overlap in the home ranges of individuals can provide indirect information about the likelihood of social interactions. We compared data on foraging and roosting range overlap of the tent-roosting bat *Artibeus watsoni* to assess how environmental and demographic factors may affect movement patterns and social interactions. We estimated the overlap of foraging and roosting ranges among simultaneously radiotagged dyads and calculated a simple association index among these individuals. We then used these data to determine whether relative population and roost abundance, as well as sex class, affected spatial and social patterns. Our results show that range overlap in *A. watsoni* significantly determines the degree to which individuals interact with each other. We also found that roosting range overlap may be a greater determinant of daytime social interactions than foraging range overlap, because roosting range overlap showed a stronger correlation with association patterns. In addition, the differences that we observed in roosting range overlap and association among dyads were a consequence of the effects of population and roost density. Bats sampled in areas of high-population abundance had significantly higher roosting range overlap than bats in areas of low-population abundance, and roosting ranges of bats sampled at sites with few roosting resources (i.e. tents) overlapped more than those of bats living in areas with more tents. Finally, we observed no overlap in roosting range and no association among adult males, supporting the hypothesis that males defend tents or roosting areas against other males to gain exclusive mating access to females using these structures.

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Use of space and ranging patterns have been critical in identifying social and mating systems in birds and mammals (Emlen & Oring 1977; Clutton-Brock 1989), and the amount of overlap in individual home ranges can provide indirect information about the likelihood of social interactions (Shier & Randall 2004). Differences in the degree of overlap in home ranges may not only be influenced by resource abundance and dispersion, but

also by the independent and combined effects of demography and social affinities. For example, reduced mobility, and a subsequent increase in overlap of individual home ranges, may occur in response to high-population densities (Ferron & Ouellet 1989; Nielsen & Woolf 2001; Dahle & Swenson 2003; Steury & Murray 2003; Linders et al. 2004; Schradin & Pillay 2005; Viggers & Hearn 2005), whereas a reduction in overlap may occur in territorial species that defend their ranges against intruding conspecifics (Brown & Orians 1970; Maher & Lott 1995). In contrast, range overlap in some species is greater among closely related individuals (Albon et al. 1992; Ratnayeke et al. 2002), and spatial proximity between males and females may increase during the breeding season (Fisher & Lara 1999; Shier & Randall 2004), indicating that social attraction may also influence range overlap.

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Resource abundance has been documented to have a significant effect on range overlap (e.g. Carpenter & MacMillen 1976; Ewald & Carpenter 1978; Gass 1979; Frost & Frost 1980; Carpenter 1987; Armstrong 1991; Maher & Lott 2000), and may ultimately be a major force favouring, or hindering, social interactions. For example, the relationship between food quantity and range overlap, or territoriality, is known to have an inverted U shape (Brown 1964; Gill & Wolf 1975; Carpenter & MacMillen 1976; Maher & Lott 2000; McLoughlin et al. 2000). This means that when food abundance is low, the costs of defending resources are higher than the energy yielded by these resources, and thus an increase in overlap can be expected. The cost–benefit ratio shifts towards territoriality, or overlap reduction, as resources increase, although if these resources become abundant, the cost of defending them against intruders becomes too high, and territoriality decreases again. Thus, if resource availability is an essential factor influencing territoriality, divergence in range overlap should occur among individuals residing in areas of differing resource distribution and abundance (Carpenter & MacMillen 1976).

In this study we used estimates of range overlap in the tent-making bat *Artibeus watsoni* to test the hypothesis that dyads sharing a larger proportion of their foraging and/or roosting range have an increased likelihood of association. In addition, we examined how relative population and roost abundance, as well as sex class, may influence association among individuals through its effect on ranging patterns and territoriality. *Artibeus watsoni* is a small (ca. 11 g) phyllostomid bat that ranges from Veracruz, México through Central America to Colombia. It is usually found below elevations of 800 m in semideciduous and evergreen lowland forests, second growth, and fruit groves (Reid 1997). It feeds primarily on fruits, although to a lesser extent may consume insects and pollen (LaVal & 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 & Lumsden 2003). In Corcovado National Park and in the Golfito Wildlife Refuge, located in southwestern Costa Rica, *A. watsoni* roosts commonly in plants such as *Carludovica palmata*, *Asplundia alata*, *Heliconia imbricata* and *Calathea lutea*, which appear to be modified into tents by males (Chaverri & Kunz 2006). These males, and the accompanying females, show different tent fidelity indexes and plant preferences among study sites, most likely as a consequence of human activities and their effect on the local roosting resources (Chaverri & Kunz 2006).

METHODS

This study was conducted at two protected areas in southwestern Costa Rica during June 2003–March 2005. Corcovado National Park (8°28'N, 83°35'W) is a 42 468-ha park with altitudes ranging from sea level to 550 m, and the Golfito Wildlife Refuge (8°38'N, 83°11'W), which comprises 2810 ha, has altitudes that range from sea level to 505 m. Within Corcovado, we sampled populations at five different sites, all near the Sirena Research Station.

Two of these sites, Mirador de Orero (MO) and Danta Primario (DP), were in undisturbed primary forests, and one site, Espavel (ES), was mostly in primary forest, although late secondary forests were also adjacent to this site. Two other sites, Naranjo 1 (NA1) and Naranjo 2 (NA2), were in secondary forests. Bats in Golfito were sampled from two 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 first site was located in a cacao plantation (CT) mixed with bananas and other exotic fruit-bearing trees near the Playa Cacao sector. The second site was located in an abandoned bamboo plantation (BO), which contained abundant pioneer understory plants. The two main study areas, Corcovado and Golfito, were approximately 26 km apart, and the average \pm SD distance between sites within these two main areas was 518.87 ± 229.65 m (range 254.77–886.83). Finally, the size of the sites surveyed ranged from 0.16 to 0.94 ha, with an average of 0.42 ± 0.27 ha.

Foraging and Roosting Range Overlap

To estimate range overlap, we captured individuals during the day at their roosts using hand nets with extendable poles (Kunz & Kurta 1988) and fitted individuals with unique numbered plastic wing bands (A.C. Hughes, Hampton Hill, Middlesex, U.K.), after slitting the propatagium through which the band was inserted (Kunz 1996). We then recorded length of forearm (with dial callipers, ± 0.1 mm) and body mass (with a Pesola spring scale, ± 0.5 g), and subsequently collected data on sex, age and reproductive status. We attached radiotransmitters (Holohil Systems Ltd., Woodlawn, Ontario, Canada, model BD-2 and BD-2N; 0.47–0.51 g; 3.9–4.25% of the bat's body mass) using Skin Bond Cement (Smith and Nephew United, Largo, Florida, U.S.A.) to 54 bats, and used two radioreceivers (TRX-1000S, Wildlife Materials, Inc., Carbondale, Illinois, U.S.A.) with three-element Yagi antennae to locate bats during the day and night.

To measure roosting range, we located potential roosts occupied by radiotagged bats and approached them carefully, verifying the presence of bats fitted with radiotransmitters using binoculars. We then recorded which radiotagged individuals occupied the same roost, and whether other untagged bats were also using this roost, and subsequently marked tents with plastic flagging tape and individually numbered aluminium tags. Finally, we recorded tent location using a Global Positioning System (eTrex, Garmin International Inc., Olathe, Kansas, U.S.A.). Bats were located in their tent roosts as long as the radiotransmitter remained active (5–17 days) and attached to the bats.

To assess foraging range, we obtained location fixes at night using both radioreceivers. We recorded bearings as soon as the radiotagged bats began their nightly activities (ca. 1800 hours), and obtained fixes approximately every 5 min during peak activity. This interval was enough for the bats to traverse their entire home range, although after peak activity, bats often stayed longer at the same

location; thus, we recorded data as soon as possible after we noticed considerable movement (i.e. the bat was flying or the resulting bearings were more than 15° apart from the previously recorded bearing). The Arithmetic Mean Estimator in LOAS software (version 3.0.1, Ecological Software Solutions, Urnäsch, Switzerland) was used to estimate bats' locations during the night, and the Home Range Extension (Rogers & Carr 1998) in ArcView software (Environmental Systems Research Institute, Redlands, California, U.S.A.) was used to estimate the 100% minimum convex polygons for foraging and roosting ranges.

Overlap in foraging and roosting range between two individual bats was estimated by first calculating the size of the overlapping region in ArcView. Percentage range overlap was then calculated using the formula $(R_{ij}/R_i + R_j) \times 2$, where R_{ij} represents the size of the region of overlap between bats i and j , and R_i and R_j represent the total range size of bats i and j . By multiplying this number by 2, we obtained the average size of overlap within each bat's range. We only calculated overlap in foraging and roosting range for dyads radiotracked within the same study site and period.

Patterns of Association

Bats were considered to be associating if they were observed roosting in the same tent at the same time, and so we only considered in our analyses associations occurring at the roost during the daytime. Roosting associations are important in understanding social behaviour because many bats engage in social interactions, such as mating and rearing young, almost exclusively at their roosts (Kunz & Lumsden 2003), potentially leading to a considerable effect of roosting behaviour on social strategies.

To determine patterns of association among dyads in MO, DP, ES, NA1, NA2, CT and BO, we used the simple ratio association index (Cairns & Schwager 1987; Ginsberg & Young 1992). This index was calculated as $X/(X + Y_{AB} + Y_A + Y_B)$, where X is the number of observations during which bat A and bat B were observed together in the same roost, Y_{AB} is the number of observation periods during which A and B were observed in separate groups, Y_A is the number of observation periods during which only A was observed, and Y_B the number of observations in which only B was observed. We also used average linkage cluster analysis (Morgan et al. 1976; Whitehead 1997) to visualize patterns of association among radiotagged individuals, and only performed such analysis for the areas where radiotracking was performed simultaneously on a large sample of the social group under study, specifically in MO and NA1.

Statistical Analyses

We classified sites within Corcovado and Golfito based on the relative abundance of individuals and roosts observed during our study. 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.

Estimates of relative abundance for all sites were then transformed into three categories using SPSS version 10 (SPSS Inc., Chicago, Illinois, U.S.A.). While estimating relative 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. The validity of this classification system for relative abundance estimates in our study was supported by roost survey data, which showed that encounter rates with roosting bats were high in areas classified as having high relative abundance and low in areas of low relative abundance. However, we minimized potential biases of our mist-netting sessions by assigning sites to broader categories instead of using the measurement data of bats per net-hour.

Relative roost abundance was estimated based on the number of tents used by all simultaneously radiotagged individuals, and the number of tents per site was transformed into three categories using SPSS. Although this assessment of roost abundance may underestimate actual availability of roosts per unit area, we decided to use this variable because modified leaves were more often found in areas that we classified as having high roost abundance, whereas tents were seldom observed in areas of low roost abundance. To minimize potential biases in our estimates of roost abundance, we assigned sites to broader categories instead of using measurement data of total tents per site.

Three univariate, nonorthogonal, three-factor-weighted general linear models (GLM; Timm & Mieczkowski 1997) were used to determine the effect of relative population abundance, relative roost abundance and sex on foraging and roosting range overlap and association patterns. If tests of within-subjects effects were significant, we used Tukey's pairwise comparison at an alpha of 0.05 to identify differences within factors. In addition, we used a Mantel test to examine a possible correlation between association indexes and range overlap among bat dyads. All analyses of associations, including the Mantel test, were performed in SocProg version 2.2 (Whitehead 1999). SPSS version 10 (SPSS Inc., Chicago, Illinois, U.S.A.) and SAS version 8.1 (SAS Institute Inc., Cary, North Carolina, U.S.A.) were used in all other statistical analyses. Values reported are means ± SD, and significance was assessed at an alpha of 0.05.

RESULTS

During the 22-month study period, encompassing both the mating and nonmating seasons, we recorded more than 30 night fixes each on 42 individuals, 16 males and 26 females. The other 12 bats either lost their radio-transmitter before we were able to obtain a large enough sample, or the transmitter ceased functioning properly after just a few days. We also excluded from the analyses of range overlap and association patterns juveniles and subadults, as well as satellite males (defined here as adult males located in areas where females were never captured).

Thus, we present data for a total of 33 bats, 10 males and 23 females, which had an average \pm SD of 57.3 ± 13.61 night radiofixes per bat (range 31–92). At night, bats were tracked for an average \pm SD of 13.9 ± 4.5 h (range 3.5–21), and for 5.7 ± 1.1 days (range 4–8). Additionally, we were able to locate these 33 bats while they were roosting for an average of 9.85 ± 2.61 days (range 5–17).

The univariate general linear model was significant for overlap of foraging range ($R^2 = 0.47$, $F_{11,43} = 2.52$, $P = 0.02$) and for overlap of roosting range ($R^2 = 0.46$, $F_{11,43} = 2.38$, $P = 0.02$), but was not significant for association patterns ($R^2 = 0.34$, $F_{11,43} = 1.44$, $P = 0.20$). We found a significant effect of relative roost abundance on overlap of foraging and roosting range (Table 1), and relative population abundance had a significant effect on overlap of roosting range but not on overlap of foraging range. Bat dyads sampled in areas of high relative population abundance had significantly more overlap in roosting range than bats in areas with medium population abundance (Fig. 1a). Foraging and roosting range overlapped significantly more between bat dyads sampled from areas of low relative roost abundance (Fig. 1b). Finally, we found no significant differences in overlap in roosting or foraging range among sex-class dyads ($F_{2,31} = 1.45$, $P = 0.24$; Fig. 1c), but roosting range did not overlap among any of the adult males sampled.

Cluster analysis of dyadic simple index associations indicated that, within social groups surveyed during the radiotracking period, individuals were observed roosting most often with the same group members. For example, in MO the female dyad 1563–1564 and the male–female dyad 1560–1561 were observed roosting together 50% of the time (Fig. 2), whereas the female–male dyads 1786–1787 and 1621–1641 in the NA1 colony were observed roosting together more than 80% of the time (Fig. 2). Male–male dyads never associated, but the cluster analysis assigned a low association index to these since males were often observed roosting with some of the same females. In addition, we never captured more than one adult male in a single group ($N = 241$), except in dyads sampled in areas where females were absent. The cluster diagram also showed that bats in MO, a site with high roost abundance and high relative population abundance, had lower association indexes than bats sampled in areas of lower roost and population abundance, such as NA1.

We found a significant positive correlation between association levels and overlap in foraging range (Mantel

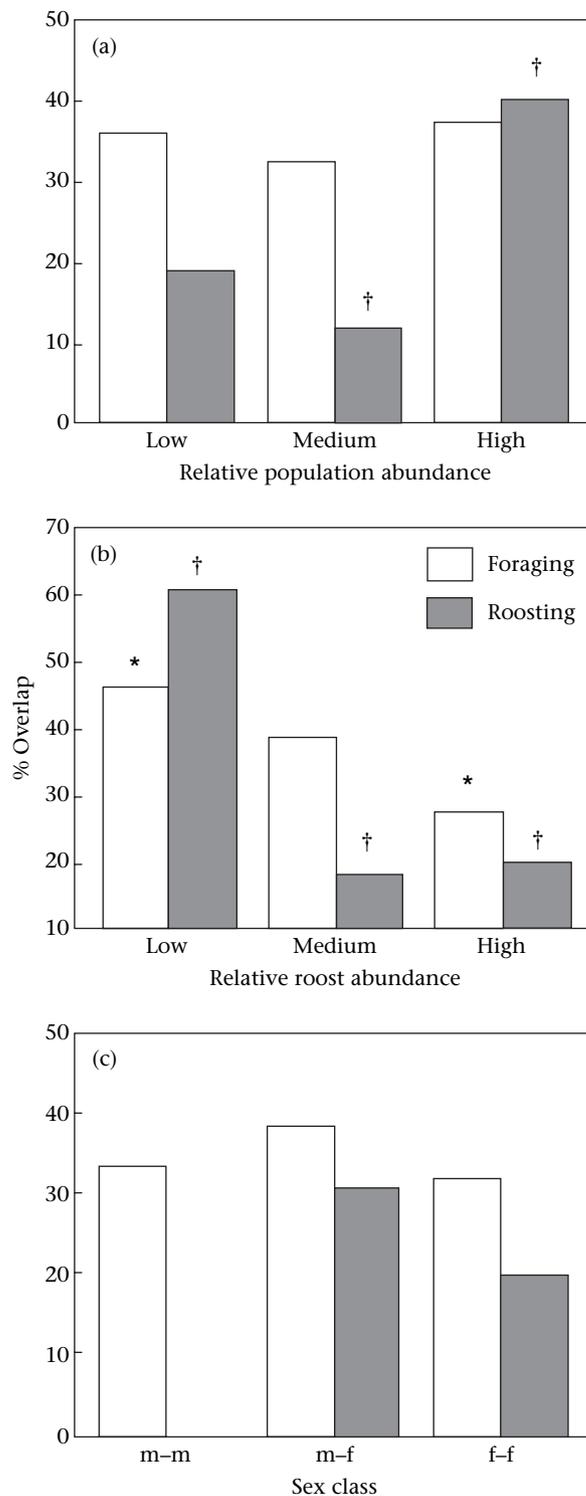


Table 1. Summary of relevant statistics generated from the nonorthogonal, three-factor general linear model

Factor	Overlap in foraging range		Overlap in roosting range	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Relative population abundance	0.58	0.56	4.19	0.02
Relative roost abundance	6.46	0.005	5.96	0.006
Sex	1.34	0.27	1.63	0.21

Figure 1. Mean percentage overlap in foraging range and roosting range among areas of variable relative population densities (a), among areas of variable relative roost abundance (b) and among sex classes (c). Significant differences ($P < 0.05$) among categories are indicated by the symbols * and †.

Z test: $r = 0.12$, $N = 33$, $P < 0.01$; Fig. 3a) and roosting range ($r = 0.82$, $P < 0.01$; Fig. 3b) among radiotagged dyads. Thus, two bats whose foraging and roosting ranges overlapped little were seldom observed roosting together,

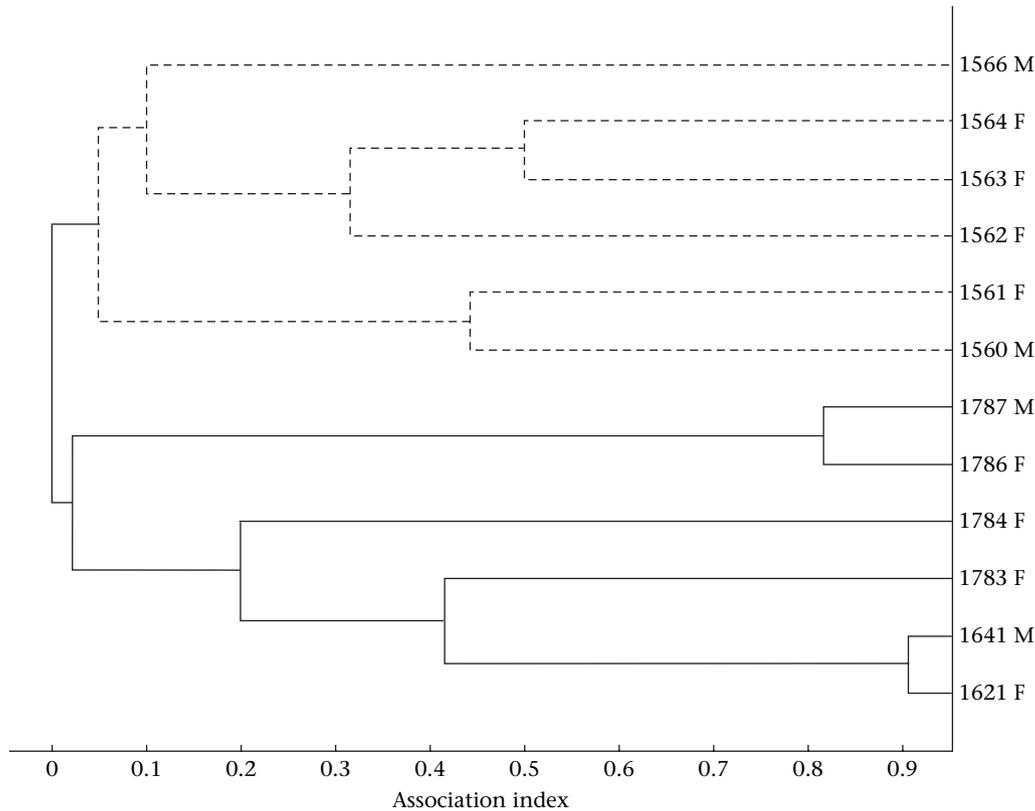


Figure 2. Hierarchical cluster diagram of simple ratio association indexes of bats radiotracked at two sites in Corcovado National Park, Costa Rica: NA1 (dashed line) and MO (solid line).

whereas bats with increasing range overlap had correspondingly high association levels. However, the correlation coefficients indicated a stronger relationship between roosting range overlap and association values, and a weaker relationship between foraging range overlap and association values.

DISCUSSION

Our results show a strong relationship between roosting and foraging range overlap and association patterns in *A. watsoni*, reinforcing the hypothesis that social interactions in mammals are greatly influenced by space use (Clutton-Brock 1989). Our results also show that overlap in roosting range may affect social interactions more than does overlap in foraging range, because roosting range showed a stronger correlation with association patterns. This finding may be the result of our choice of methods, because we were only addressing interaction among individuals during the daytime, even though bats are known to interact with other individuals in night roosts as well (Kunz 1982). Thus, a stronger relationship between roosting ranges and interaction levels is a probable outcome of the methods we used to understand social behaviour in *A. watsoni*. Roosting associations are important in understanding social behaviour in this species, however, because mating and rearing young occurs almost exclusively at the roost (Chaverri & Kunz 2006, in press), potentially leading to a considerable effect of roosting behaviour on social tactics.

A potential disadvantage of explaining roosting associations in *A. watsoni* through patterns of space use is that spatial overlap evidently increases the chances of individuals coming into contact. However, the fact that bats shared the same tents at the same time, even when roosts were readily available, is clear evidence of the gregarious nature of this species, and the degree to which individuals share roosts in different areas provides an important means of understanding the costs and benefits of sociality. Therefore, understanding how individuals move around roosting and foraging areas, and whether that use of space correlates with the likelihood of association, provides valuable information on the effect of ecological factors on social interactions.

Factors Influencing Range Overlap and Association Patterns

Our results indicate that the differences observed in roosting range overlap among dyads were largely a consequence of relative population and roost abundance. Bats sampled in areas of higher relative population abundance, for example, had significantly higher overlap in roost and foraging ranges than did bats in areas of lower population abundance. Moreover, roosting range overlapped significantly more among bats sampled in areas of low roost abundance compared to bats from areas of medium or higher roost abundance. This suggests that when roost abundance is too low, or when resources must be shared

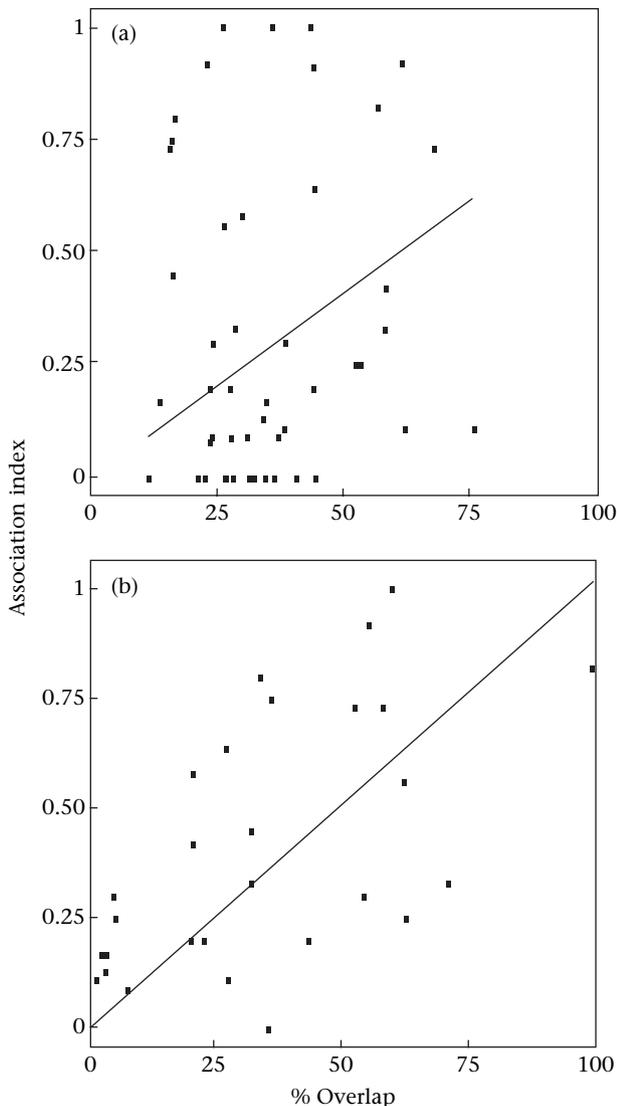


Figure 3. Relationships between simple ratio association indexes and percentage overlap in foraging (a) and roosting range (b) among simultaneously radiotagged bat dyads.

among more individuals, the costs of defending resources may be too high, causing an increase in range overlap. The cost–benefit ratio shifts towards territoriality, or overlap reduction, as resources increase or as populations decrease in size, as has been previously observed for food quantity and territoriality in other organisms (Brown 1964; Gill & Wolf 1975; Carpenter & MacMillen 1976; McLoughlin et al. 2000; Maher & Lott 2000).

We observed no significant differences in overlap of foraging range among areas of variable population abundance, but we found a significant effect of roost abundance on foraging ranges. Population density is known to influence territoriality in many species (reviewed in Maher & Lott 2000; Morrell & Kokko 2005), indicating that intruder pressure and its effect on local resources is an important factor influencing movement patterns. However, in *A. watsoni* we did not observe a change in foraging range overlap among sites with

variable population abundance, most likely because food is not a limiting resource for this bat. Although *A. watsoni* is known to use more plant species for roosting than any other tent-roosting species (Kunz & Lumsden 2003; Chaverri & Kunz 2006), adults roost exclusively under leaves that require a substantial energetic investment to modify into tents. In contrast, this bat feeds on more than 30 fruit species at one particular site (G. Chaverri, unpublished data), and the fruits consumed by this bat are abundant in many habitats, such as plantations and forests in early and late stages of regeneration. This finding suggests that tents are a more limited resource for *A. watsoni* than are the fruits they feed upon, and that availability of roosts may influence territoriality more than does the availability of food.

Our observation of a strong correlation between range overlap and association patterns in *A. watsoni* suggests that the same factors influencing range overlap, namely roost abundance, population abundance and sex class, are likely to be responsible for the differences in association patterns observed between individuals. However, association patterns of other bat species are not known to be influenced by resource availability (e.g. Vonhof et al. 2004), and individuals may remain together more often if they are genetically related (Rossiter et al. 2002; Ortega et al. 2003), or if they are in the same reproductive condition (Lewis 1996; Kerth & König 1999). In *A. watsoni*, however, clustering at particular roosting sites seems to be, at least in part, a consequence of the aggregation of individuals at preferred roosting and/or foraging areas. Thus, *A. watsoni* may initially select areas that provide suitable foraging and roosting resources, and then aggregate with other individuals using those same areas, although it is possible that other factors, such as relatedness and reproductive status, may increase fidelity to particular individuals.

Male Territoriality

Even though sex class did not have a significant effect on roosting and foraging range overlap, we observed no overlap in roosting range between male–male dyads. Therefore, we suggest that the lack of overlap among males is a consequence of territoriality that facilitates defence of critical and energetically expensive roost resources. Indirect evidence of roost construction in *A. watsoni* (Chaverri & Kunz 2006) and direct observations of leaf modification in other tent-roosting species (Balasingh et al. 1995; Muñoz-Romo & Herrera 2003) suggest that males are largely responsible for leaf modification. Since adult females of *A. watsoni* only roost in modified leaves (Chaverri & Kunz 2006), males most likely construct and/or defend these structures to attract females, and then mate repeatedly with them at the roost. It is possible, then, that males construct tents within a relatively small area, and defend this area against intrusions by other adult males.

The most common definition of territoriality is the defence of space (Maher & Lott 1995). Individuals may defend the entire home range, or defence may be limited to mating spots, nests, feeding areas or roosts (Brown & Orians

1970). In small and secretive species, however, it is often challenging to observe instances of aggressive interactions, and thus other approaches are necessary to determine whether territoriality exists or not. Range overlap, for example, is a preferred option for researchers studying mammals (Maher & Lott 1995), and exclusive use of an area, with little or no overlap among individuals or groups, is generally considered to reflect territoriality. Thus, the lack of roosting range overlap and association among resident males should be a strong indication of territoriality in *A. watsoni*. Additionally, satellite males, or males located in areas where females were never captured, were often observed roosting together, showing that when roosts are not used to attract females, territorial behaviours may decrease, as has been observed in the insectivorous bat *Saccopteryx bilineata* (Heckel & von Helversen 2002).

In conclusion, we have shown that ranging patterns significantly influence association patterns in *A. watsoni*, and that overlap in roosting range may influence interactions among individuals more than overlap in foraging range. Our results also show that population and roost abundance are important factors influencing range overlap, although these variables may have a stronger effect on overlap in roosting range owing to the scarcity of tents compared to feeding resources. We found that neither population nor roost abundance had an effect on association patterns, indicating that other factors may influence fidelity to particular individuals, not only the environmental and demographic conditions of an area. We also observed no overlap in roosting range and no association among adult males, suggesting that males defend tents or roosting areas against other males to gain exclusive mating access to females using these structures. This study also demonstrates that behavioural models generated for terrestrial mammals, particularly regarding ranging and association patterns, may also allow us to accurately predict social tactics in bats, even though bats' life history traits do not conform to typical mammalian patterns (Jones & MacLarnon 2001; Barclay & Harder 2003). Therefore, our study provides an initial attempt to understand how ecological factors, such as resource abundance and population density, affect bats' behavioural decisions, and how these decisions are similar to those of other mammalian taxa.

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