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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.

Keywords: *Artibeus watsoni*; association patterns; range overlap; tent-making bat; territoriality

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 ± 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