

## MATING SYSTEM OF THE TENT-MAKING BAT *ARTIBEUS WATSONI* (CHIROPTERA: PHYLLOSTOMIDAE)

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Vertebrate mating systems are influenced by ecological and phylogenetic factors, and the variation observed in mating behavior is frequently attributable to the extent to which male assistance in the rearing of offspring increases a female's reproductive rate, size and stability of female groups, and density and distribution of females in space. In this study we evaluate patterns of association and parentage to describe the mating system of the tent-making bat *Artibeus watsoni*. During 16 consecutive months, we regularly surveyed 2 sites in southwestern Costa Rica and determined size, composition, and stability of social groups, and established patterns of parentage within roosts. We found female-biased, mixed-sex social groups formed by individuals located in several roosts within an area. Roosting associations were low (average across all sites: 31%), and the frequent changes between roosting partners suggests that males and females formed nonexclusive mating bonds, which was further supported by our finding that only 27% of young were sired by the male within a roosting group. Paternal sibships were only observed in 17% of dyads of young roosting together, indicating that few males copulated with >1 female of the roosting group during the mating season. However, paternal sibships were only observed in Golfito, which could be explained by greater group size and stability attributable to lower roost availability. Thus, our findings are consistent with a polygynandrous mating system (2 or several males sharing access to 2 or several females, and vice versa) in which males associated intermittently with females that frequently switched roosts, and where breeding opportunities for males seemed related to the defense of roosts, roosting territories, or both.

Key words: paternity, patterns of association, polygynandry

Theories suggest that vertebrate mating systems are influenced by ecological and phylogenetic factors (Clutton-Brock 1989; Crook et al. 1976; Emlen and Oring 1977), and that variation observed in mating behavior between species is frequently attributable to the extent to which male assistance in the rearing of offspring increases a female's reproductive rate, size and stability of female groups, and density and distribution of females in space (Clutton-Brock 1989; Crook et al. 1976; Wittenberger 1980; Zeveloff and Boyce 1980). Although these theories have been and continue to be widely promoted to help advance understanding of mating strategies, they do not consider the role of a male's behavior on female fitness and the female's response to male distribution (Alonzo 2007), implying a minor role of female choice over mating partners. In addition, vertebrate social and mating systems are often regarded as fixed species attributes, even though there is an increasing body of evidence demonstrating variation in social and mating behavior within species (e.g., Charmantier and

Perret 2004; Davies and Lundberg 1984; Martin and Martin 2007; Owens and Bennett 1997; Pemberton et al. 1999; Randall et al. 2002; Travis et al. 1995; Warner and Hoffman 1980).

Polygyny, a mating system in which males mate with the same group of females in successive mating attempts, is the most common mating system found among mammals (Clutton-Brock 1989; Kleiman 1977), including bats (McCracken and Wilkinson 2000); presumably this is because males are able to associate with several mating partners given their limited role in offspring care (Orians 1969) and because environmental conditions favor the clumping of females around critical resources such as food and nests (Emlen and Oring 1977). Monogamy, a mating system in which males mate with a single female, has traditionally been viewed as the most common mating system in birds (Greenwood 1980; Orians 1969), yet it is relatively rare in mammals (Clutton-Brock 1989; Kleiman 1977). Another uncommon mating system in mammals is promiscuity, in which males mate with any receptive female and there is no continuing bond between males and females after mating occurred (Clutton-Brock 1989). However, these classifications of mating systems only explain the reproductive behavior of males, and even though we still know very little about the number of mating partners that females have, mating systems of females are classified in a way similar to those of

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males. For example, females may be monogamous when they mate exclusively or almost exclusively with a single male during 1 reproductive period, polyandrous when they mate with a restricted group of the same males in successive breeding attempts, and promiscuous when they mate with different males in successive breeding attempts (Clutton-Brock 1989).

With the advent of genetic and computational methods, our knowledge of social organization and mating systems in bats has greatly increased. For example, the use of molecular techniques has allowed us to understand offspring dispersal (Dechmann et al. 2007), paternity, and reproductive success (Heckel and von Helversen 2002; Heckel et al. 1999; Rossiter et al. 2000), sperm competition (Hosken 1998), colony relatedness and kinship (Kerth et al. 2002; Rossiter et al. 2002), inbreeding (Rossiter et al. 2005), and the effect of environmental variability on mating success (Storz et al. 2001). Similarly, recent computational methods used in the analysis of interactions among individuals in social groups allow us to carefully examine community size, typical group size, stability of associations, modularity, and linearity of dominance, among others (Whitehead 2008), which are important to understand because these interactions form the basis of any social structure (Hinde 1976). In this study, we used some of these advances, particularly indices of association, to establish group stability and size, and genetic markers to understand patterns of parentage, to describe the mating system of the tent-making bat *Artibeus watsoni*.

*Artibeus watsoni* is a small (about 11 g) phyllostomid bat that usually can be found below 800 m elevation, in semideciduous and evergreen lowland forests, 2nd growth, and fruit groves (Reid 1997). It feeds primarily on fruits, although insects and pollen also are consumed (LaVal and Rodríguez-H. 2002). *A. watsoni* has a seasonal bimodal polyestry, wherein mating occurs primarily in late November, December, and then again after the 1st parturition period in late February–early March (Chaverri and Kunz 2006a). This species roosts beneath modified leaves and is known to use more plant species for roosting than any other tent-making bat (Kunz and Lumsden 2003). Males and females usually exhibit low roost fidelity, although they use roosts intermittently in a relatively restricted area (Chaverri and Kunz 2006b). Tents are never simultaneously occupied by >1 adult male (Chaverri et al. 2007a), and males appear to be primarily responsible for roost construction (Chaverri and Kunz 2006b). Thus, males probably engage in territorial behavior to defend roosts or roosting areas and, because copulation occurs in the tent-roost (Chaverri and Kunz 2006a), males may gain access to breeding females that use these roosts (Chaverri et al. 2007a). In addition, previous research on *A. watsoni* in southwestern Costa Rica has shown that populations differ significantly in their abundance and roosting behavior, most likely as a result of human activities and their effect on local resources (Chaverri and Kunz 2006b).

## MATERIALS AND METHODS

Our study was conducted within 2 protected areas in southwestern Costa Rica from June 2003 through March

2005. One site, Corcovado National Park (8°28'N, 83°35'W), is a 42,468-ha area with altitudes ranging from sea level to 550 m. This site is characterized by an annual precipitation of 5,500 mm, and average temperatures range between 24°C and 28°C. This park is composed mostly of dense tropical broad-leaved evergreen lowland forests (Kappelle et al. 2002). Populations of *A. watsoni* at this site were sampled mainly in primary forests (sampling locations: Danta Primario [DP], Danta Secundario [DS], Espavel [ES], and Mirador de Orero [MO]), although some individuals also were captured in secondary forests (sampling locations: Naranjal 1 [Na1] and Naranjal 2 [Na2]). The other research site, Golfito Wildlife Refuge (8°38'N, 83°11'W), is a 2,810-ha area and ranges in altitude from sea level to 505 m. The bat population in Golfito was sampled in 2 plantations (sampling locations: Bamboo [BO], Cacao 1 [CT1], and Cacao 2 [CT2]) bordering areas that are either completely modified by humans or are in intermediate stages of regeneration. Primary forests with steep elevations of up to 230 m also surround these locations. Annual precipitation in Golfito ranges from 4,000 to 5,000 mm, with average temperatures of 24–28°C. The area is composed mostly of dense tropical broad-leaved evergreen lowland forests, but it also includes pasturelands, mangroves, forest plantations, agricultural crops, and human settlements (Kappelle et al. 2002).

*Roosting associations, stability, and seasonality.*—We captured roosting bats during the day and throughout the year using hand nets with extendable poles (Kunz and Kurta 1988) to determine roosting associations. We recorded data on group size and composition, specifically focusing on the number of adult females and males. Juveniles and subadults were distinguished from adults based on the presence of cartilaginous epiphyseal plates in metacarpals and phalanges (Anthony 1988), and juveniles could be further distinguished from subadults if the former were still nursing and roosting with their mothers. All captured bats (adults and juveniles) were then fitted with individually numbered plastic wing bands (A. C. Hughes, Hampton Hill, Middlesex, United Kingdom), with females banded on the left wing and males banded on the right wing. The edges on all plastic bands were smoothed with a file before they were applied to avoid injury to the bats. We followed guidelines of the American Society of Mammalogists (Gannon et al. 2007) for the capture, handling, and care of mammals, and all protocols were approved by the Animal Care and Use Committee at Boston University and by the Costa Rican government.

To determine short-term stability of roosting associations, we attached radiotransmitters (models BD-2 and BD-2N; 0.47–0.51 g; 3.9–4.25% of the bat's body mass; Holohil Systems Ltd., Woodlawn, Ontario, Canada) using SkinBond Adhesive (Smith and Nephew United, Largo, Florida) to a total of 33 individuals, and used a radioreceiver (TRX-1000S; Wildlife Materials, Inc., Carbondale, Illinois) with 3-element yagi antenna to locate bats during the day. The number of bats radiotagged at the same time ranged between 3 and 6, and the total number of sampling locations was 9 (3 in Golfito and 6 in Corcovado). Simultaneously radiotracked individuals were usually captured from a single roost, although on some occasions individuals were captured from different roosts

within the same study site. When radiotagged bats were located in their roosts, we recorded group composition, being careful not to disturb the bats, and noted whether other group members had radiotransmitters or wing bands. We placed individually numbered metal tags with flagging tape near the tents, but not on them to avoid disturbing the bats, for later recognition and recovery of used roosts.

We quantified association patterns among radiotagged individuals by using the simple ratio association index (Cairns and Schwager 1987; Ginsberg and 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 individuals, and we present all radiotagged individuals from all sampling locations in a single cluster diagram. Following Vonhof et al. (2004), we classify roosting groups henceforth as individuals using the same roost at the same time, and social groups as individuals that may or may not have used the same tents, but nonetheless were associated directly or indirectly with other individuals in the same area. Thus, for the purpose of our study we classify clusters with association index values  $> 0$  as social groups. Additionally, we focused our analysis of associations on the radiotagged bats and not on all bats captured within their roosts, given the low recapture rates of the latter.

To determine if roosting associations between males and females persisted during the mating and nonmating seasons and throughout the year, we performed periodic recaptures in the same sampling locations at different times throughout the year. Because the mating season of *A. watsoni* in southwestern Costa Rica occurs in November–December, and then again in February–March (with 2 parturition periods in February–March and then in June–July—Chaverri and Kunz 2006a), all adult bats sampled during these periods were considered to be mating. Thus, we assumed that most, if not all, individuals captured at all other times of year were nonmating. Although it was not possible to determine whether all individuals captured in the months of November, December, February, and March were mating or not, we analyzed male–female associations during the mating period separate from those in the presumed nonmating periods, in order to evaluate year-round patterns of association.

**Mating associations.**—To determine the genetic mating system of *A. watsoni*, we captured a total of 166 roosting bats during the 2 parturition periods of February–April and June–August, 2003–2005. Biopsy punches were taken from the plagiopatagium of all individuals and stored in a 20% dimethylsulfoxide–5 M NaCl solution for subsequent DNA analysis. DNA was then isolated using a DNeasy Tissue Kit (Qiagen Inc., Valencia, California). Six microsatellite DNA loci named AjA123, AjA40, AjA47, AjA151, AjA84, and AjA110 (Ortega et al. 2002) were amplified with Ampli Taq Gold using primer sets labeled with fluorescent dyes (FAM,

NED, PET, and VIC) in a Perkin Elmer Gene Amp PCR System 9700 (Applied Biosystems, Foster City, California). For each individual, amplification was carried out in a 16- $\mu$ l reaction containing approximately 50 ng of DNA,  $0.93\times$  buffer,  $0.75\ \mu\text{M}$  deoxynucleoside triphosphate,  $2.03\ \mu\text{M}$   $\text{MgCl}_2$  ( $2.34\ \mu\text{M}$  for AjA123), 0.06U Ampli Taq Gold,  $0.56\ \mu\text{M}$  fluorescent primer, and the same concentration of the nonfluorescent primer. A polymerase chain reaction amplification was conducted with initial denaturation at  $95^\circ\text{C}$  for 9 min, followed by 35 cycles of  $94^\circ\text{C}$  for 30 s,  $55^\circ\text{C}$  for 45 s ( $62^\circ\text{C}$  for AjA123), and  $72^\circ\text{C}$  for 50 s, with a final extension of 8 min. Polymerase chain reaction products for all 6 loci per individual were pooled for sizing on an ABI PRISM 3100 DNA sequencer (Applied Biosystems). Results were analyzed using GeneMapper, version 3.7 (Applied Biosystems).

Paternity analyses were performed separately for each study site, Golfito and Corcovado. We determined the likelihood that adult males captured with each roosting group were the fathers of the sampled young. We used the program CERVUS 3.0 (Kalinowski et al. 2007) to estimate allele frequencies, observed and expected heterozygosity, and probability of exclusion when neither parent was known and when 1 parent was known. We then ran simulations to evaluate the confidence in assignment of parentage to the most likely parent. In these simulations we used 10,000 simulated offspring and 4 candidate males, with proportion of candidate males sampled of 0.25. The proportion of loci typed used in the simulation was 0.99 (Corcovado) and 1.00 (Golfito), based on the average value across loci and individuals, and the proportion of loci mistyped was set to 0.01.

Maternity of attached and unattached young was confirmed using CERVUS for all roosting groups. After successful maternity assignment, all mother–young pairs were used to determine if males captured with the roosting group were potential fathers of the young. Males were confirmed as the father if 1 or 0 allelic mismatches occurred for all 6 loci, and if the LOD score for that male was positive. An LOD score is the natural logarithm of the product of likelihood ratios (i.e., likelihood of paternity of a randomly chosen male) across multiple loci. We verified paternity only for the adult male present at the time of capture of young because we were unable to obtain large enough samples of adult males at each site for both parturition periods. Thus, our study only addresses the question of whether a male fathered a young in its roost, providing evidence of long-term mating associations among males and females from the mating season until the parturition period (about 3 months).

To identify paternal half-siblings (i.e., young with the same father) among young roosting in the same tent, we used a likelihood-based statistical test using the program KINSHIP 1.3 (Goodnight and Queller 1999), and allele frequencies generated by CERVUS. We determined the probability that shared alleles were identical by paternal descent by testing the hypothesis that shared alleles are identical by direct descent from a common father (probability that shared alleles are identical by paternal descent [ $R_p$ ] = 0.50, probability that shared alleles are identical by maternal descent [ $R_m$ ] = 0.00).

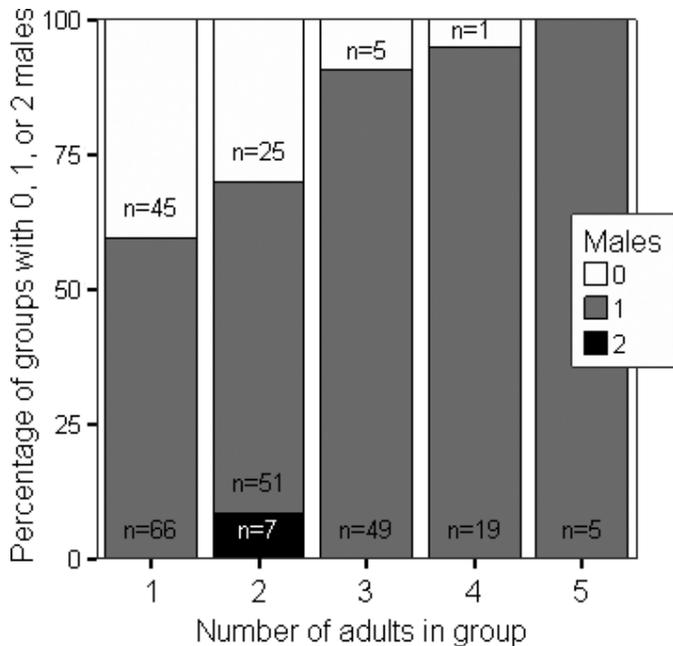


FIG. 1.—Percentage of groups that contained 0, 1, or 2 adult male *Artibeus watsoni* in roosting groups of 1–5 adults. Data are combined from all months.

The null hypothesis was that alleles are not identical by descent through either route of Mendelian transmission ( $R_p = 0.00$ ,  $R_m = 0.00$ ). Using KINSHIP, we calculated the log-likelihood ratio between the primary and null hypotheses, where high values favor the primary hypothesis and low values reject it in favor of the null hypothesis. We then performed significance calculations to associate a  $P$ -value for acceptance of the primary hypothesis for likelihood ratio of each pair by running 1,000 pairs of simulation routines. Young were identified as paternal half-siblings if  $P$  for that dyad was  $<0.05$ . The results of this analysis were used to determine if young were sired by the same male at the same roost, providing indirect evidence of male mating success within the same breeding season. We did not assess reproductive success of all males sampled in an area because of incomplete sampling of adult males and young at each site for both parturition periods. Values are given as mean  $\pm$   $SD$  unless otherwise stated.

## RESULTS

**Roosting associations.**—We captured a total of 424 roosting groups at both sites during our 16-month field study, although we were only able to determine group size and composition for 273 groups because some group members escaped before or during our capture attempts. Group size, including adults and juveniles, ranged from 1 to 8 individuals, with an average of  $2.39 \pm 1.49$ . The average number of adult bats present in the same roost was  $1.99 \pm 1.03$  (range 1–5). Many individuals captured were found roosting alone (41%,  $n = 111$ ; Fig. 1), but most bats were captured in groups of  $\geq 2$  individuals (59%,  $n = 162$ ). Most of these groups (77%,  $n = 124$ ) were composed of 1 to several females (with or without dependent young) and 1

adult male. Other groups (19%,  $n = 31$ ) were composed of only adult females, with or without dependent young. In addition, male pairs were documented in areas where adult females were absent (4%,  $n = 7$ ).

Within roosting groups, mean number of adult females per adult male was  $1.82 \pm 0.83$  (range 1–4). Size of groups with 1 male and several females did not differ significantly in the mating season (February, March, November, and December;  $1.74 \pm 0.75$ ) and nonmating season ( $1.92 \pm 0.91$ ;  $t$ -test:  $t = 1.17$ ,  $d.f. = 122$ ,  $P = 0.24$ ). In addition, the proportion of female groups that were associating with adult males increased as the number of females increased within a roost (Fig. 1). For example, 53% of groups composed of 1 female also included an adult male, whereas for groups composed of 2, 3, and 4 females, 66%, 79% and 83%, respectively, included a male. This indicates that as female numbers increased at a roost, so did the probability of finding a male roosting with those females.

Single-male–multifemale and female-only roosting groups were recorded during the entire year, although the former were less common in April and July and more common in February and December. Thus, during the months of sexual activity (February–March and November–December), single-male–multifemale groups were observed significantly more often than female-only groups ( $\chi^2 = 14.16$ ,  $d.f. = 1$ ,  $P < 0.001$ ), because 76% of groups captured were composed of 1 or several adult females and 1 adult male, and only 24% were female-only groups. Conversely, during the nonmating season, 57% of roosting groups were composed of 1 to several adult females and an adult male and 43% were female-only groups.

**Stability of roosting associations.**—Simultaneously radiotagged individuals commonly switched tents and roosting companions in the same area during the radiotracking period of 5–17 days. However, individuals continued to interact with the same group members, continuously or intermittently, despite constant movement among roosts, and a few dyads (i.e., male–female dyad 1698–1700) continued to associate 3 months after their initial capture. For example, in a 6-day period, the female–male dyad 1786–1787 was found roosting together almost every day, even though these bats moved among several roosts, and the female–male dyad 1621–1641 remained together at the same roost during those 6 days (Fig. 2). Other individuals did not associate as strongly with other group members (i.e., female 1783 and female 1784), but they still continued to associate with bats within the same study area intermittently. This indicates that social units were composed of individuals associating at several roosts in the same area, and not exclusively by individuals found within a single roost. However, it was difficult to determine with precision both size and composition of social groups, because we were unable to capture and radiotag all individuals in an area, and thus we often encountered roosting groups with new, unmarked individuals.

Cluster analysis of dyadic simple index associations indicates that simultaneously radiotagged bats sampled at the same site were observed roosting often with the same individuals (Fig. 3). For example, females 1702 and 1701 were observed roosting together approximately 80% of the time, and the female dyad 1744–1437 was associated approximately 93% of the time.

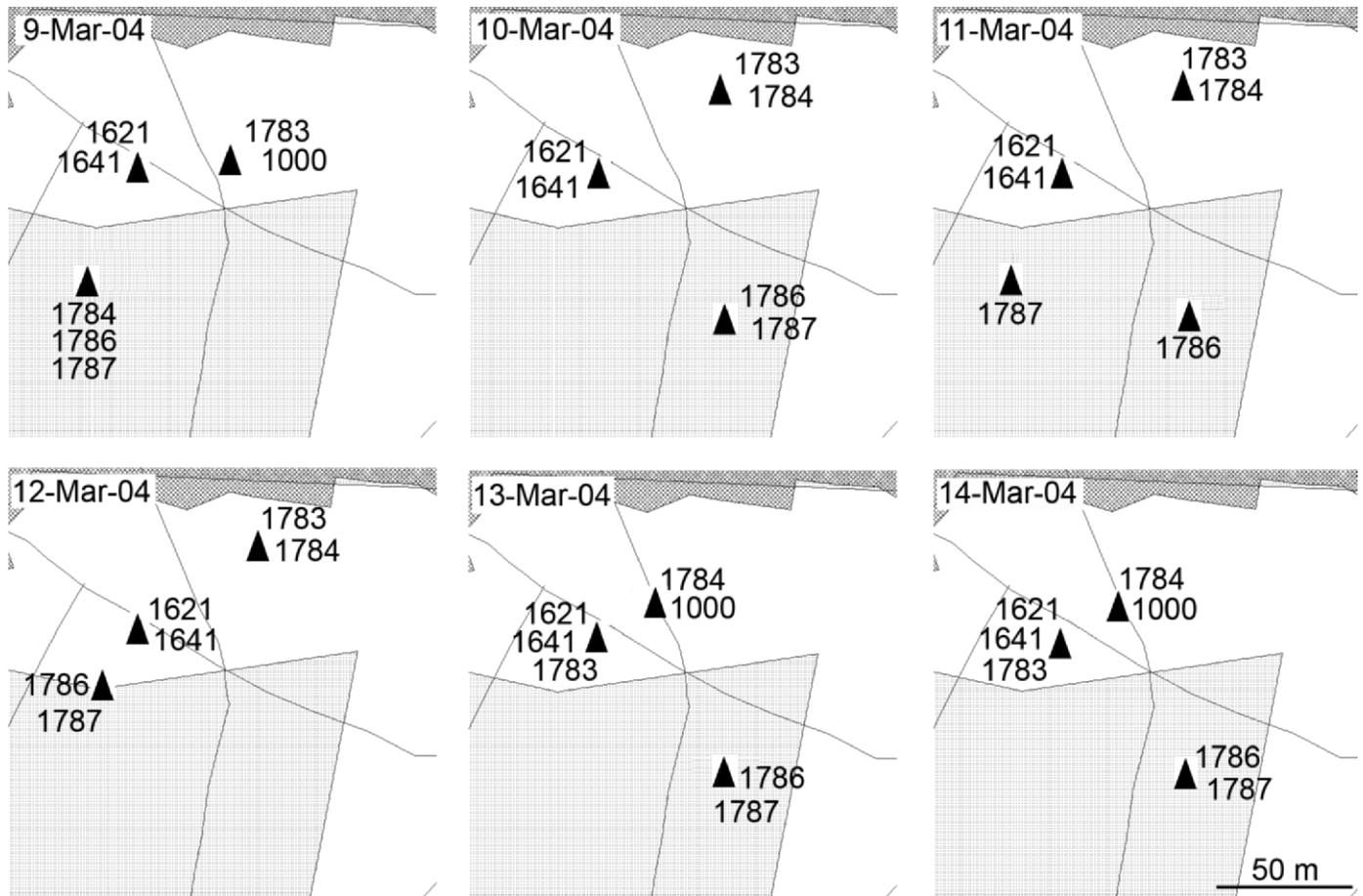


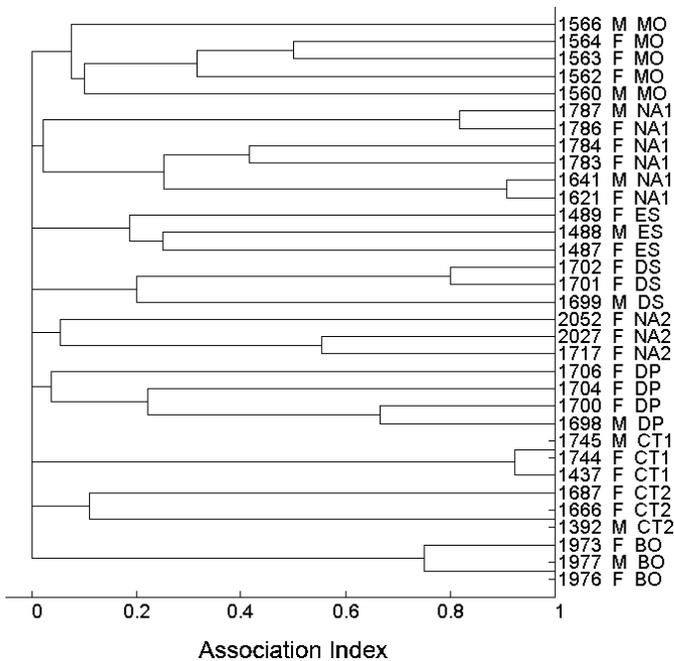
FIG. 2.—Maps representing roost location and companions of 6 radiotagged *Artibeus watsoni* for 6 days at site Naranjal 1, Corcovado National Park, Costa Rica. Triangles indicate roosts, and 4-digit numbers represent individuals observed in that roost. Bat 1000 was an unmarked individual(s). See Fig. 3 for sex of individuals. Areas in maps indicate habitats regenerating since 1970 (light gray), 1976 (white), and 1980 (dark gray). Lines represent trails.

Some male–female dyads, such as 1977–1976, 1745–1744, and 1392–1666 were always found roosting together, whereas radiotagged male–male dyads never associated. Despite these strong associations among some individuals, the mean simple ratio association index for simultaneously radiotagged bat dyads associating at the same site was  $0.31 \pm 0.33$  (range 0.00–1.00), which indicates that the same 2 individuals were observed roosting together on average 31% of the time in which they were radiotracked. However, the large variation in association indices indicates that although some dyads remained together all the time, some individuals either switched roosting groups often or never associated with some of their previous roost companions. Mean association indices for male–female dyads were larger compared to female–female dyads (male–female: overall  $\bar{X} = 0.35 \pm 0.37$ ; female–female: overall  $\bar{X} = 0.29 \pm 0.28$ ; Table 1), except for bats sampled at the sampling location Danta Secundario, in Corcovado. However, the difference in mean association index between sex classes was not significant (analysis of variance [ANOVA]:  $F = 1.08$ ,  $df = 2, 46$ ,  $P = 0.34$ ). In addition, mean association indices varied considerably between sampling locations. For example, although individuals in Cacao 1, in Golfito, were observed

roosting together on average 95% of the time, in Mirador de Orero, in Corcovado, individuals remained together only 17% of the time. Overall, bats sampled in Golfito showed significantly larger association indices compared to bats in Corcovado (for Golfito,  $\bar{X} = 0.73 \pm 0.36$ ; for Corcovado,  $\bar{X} = 0.22 \pm 0.25$ ; ANOVA:  $F = 25.39$ ,  $df = 1, 47$ ,  $P < 0.001$ ).

*Mating associations.*—Genetic analyses of paternity and pedigree relationships were conducted on a total of 87 bats from Golfito and 79 from Corcovado. In Golfito we captured 14 adult males, 37 adult females, and 36 juveniles, which belonged to a total of 20 roosting groups (Table 2). In Corcovado, we captured 16 adult males, 28 adult females, and 35 juveniles, belonging to 24 roosting groups. Paternity of the male within the roosting group was estimated for the 33 groups that contained adult males at both sites (Table 2), and analyses of paternal half-siblings were performed for dyads of young from groups where 2 or more young were present at the time of capture ( $n = 22$  groups).

Genotyping of all 6 loci revealed high allelic diversity and heterozygosity for both study sites (Table 3), resulting in high exclusionary power. Allele diversity and heterozygosity were greater in Golfito, resulting in slightly greater exclusionary



**FIG. 3.**—Hierarchical cluster diagram of simple ratio association index values for all radiotracked *Artibeus watsoni*. Individuals are indicated by identification numbers, sex (M = males; F = females), and sampling location, as described in the “Materials and Methods.” Clusters with association index values > 0 represent social groups. Short lines represent association indices of 1.

power at this site. In addition, comparison of allelic and genotypic frequencies indicates that null alleles were either absent or present at negligible frequencies in both populations (Table 3). Four mismatches at individual loci between young and mother were observed in Golfito, and 3 mismatches in Corcovado, generating average error rates across loci of 0.025 and 0.019, respectively. All mother–young pairs were successfully sampled in Golfito, but we were unable to capture the mother of 4 young in Corcovado.

Paternity was assigned to males captured with the roosting group for 12 (27%) of 45 young. Thirty-three juveniles were not assigned to the roosting male, and represent 73% of all young tested. The difference in the proportion of paternities assigned to the males among sites was not significant ( $\chi^2 = 0.36, df. = 1, P = 0.36$ ), although a slightly higher proportion of young were sired by the males in Corcovado. Most juveniles in 1-young or 2-young groups were not sired by the male (Fig. 4), and when paternity was assigned to the male, it was rarely assigned to more than 1 young within the roosting group. Nonetheless, we captured a group with 2 young in which the male had sired both young (Fig. 4). In the only 3-young group captured with an adult male, none of the young were assigned to that male.

Across all sampled young, a total of 5 dyads of young (17%) were identified as paternal half-siblings based on the significance calculations in KINSHIP ( $P < 0.05$ ). The other 83% of dyads had  $P$ -values  $> 0.05$ , indicating that they were not likely to be paternal half-siblings. Half-siblings were only observed in Golfito, and the difference in the proportion of paternal sibships among sites was borderline significant ( $\chi^2 =$

**TABLE 1.**—Mean and maximum simple index association values within and between sex classes (M = male; F = female) for all social groups of *Artibeus watsoni* sampled in Golfito and Corcovado, southwestern Costa Rica. Sample size ( $n$ ) indicates number of dyads sampled in that sex class for a particular site.

Site	Sex class	$n$	Association index	
			$\bar{X}$ (SD)	Maximum (SD)
<b>Golfito</b>				
Bamboo	M-M	0		
	M-F	2	0.88 (0.00)	1.00 (0.00)
	F-F	1	0.75	0.75
	Overall	3	0.83 (0.07)	0.92 (0.14)
Cacao 1	M-M	0		
	M-F	2	0.96 (0.00)	1.00 (0.00)
	F-F	1	0.92	0.92
	Overall	3	0.95 (0.02)	0.97 (0.04)
Cacao 2	M-M	0		
	M-F	2	0.56 (0.00)	1.00 (0.00)
	F-F	1	0.11	0.11
	Overall	3	0.41 (0.26)	0.70 (0.51)
<b>Corcovado</b>				
Danta Primario	M-M	0		
	M-F	3	0.30 (0.00)	0.67 (0.00)
	F-F	3	0.11 (0.06)	0.19 (0.06)
	Overall	6	0.20 (0.12)	0.42 (0.29)
Danta Secundario	M-M	0		
	M-F	2	0.20 (0.00)	0.20 (0.00)
	F-F	1	0.80	0.80
	Overall	3	0.40 (0.17)	0.60 (0.35)
Espavel	M-M	0		
	M-F	2	0.25 (0.00)	0.25 (0.00)
	F-F	1	0.13	0.13
	Overall	3	0.21 (0.04)	0.25 (0.07)
Mirador de Oreero	M-M	1	0.00	0.00
	M-F	6	0.10 (0.10)	0.25 (0.07)
	F-F	3	0.38 (0.05)	0.44 (0.10)
	Overall	10	0.17 (0.10)	0.37 (0.13)
Naranjal 1	M-M	1	0.00	0.00
	M-F	8	0.29 (0.09)	0.86 (0.06)
	F-F	6	0.17 (0.10)	0.34 (0.16)
	Overall	15	0.22 (0.06)	0.71 (0.23)
Naranjal 2	M-M	0		
	M-F	0		
	F-F	3	0.22 (0.15)	0.41 (0.26)
	Overall	3	0.22 (0.15)	0.41 (0.26)

3.6,  $df. = 1, P = 0.05$ ). Thirteen percent of groups composed of a dyad of young contained a paternal sibship (Fig. 5), and 33% of groups composed of 3 young had 1 paternal sibship. The only group composed of 4 young had 2 paternal sibships confirmed by KINSHIP (siblings 1305–1320 and 1314–1320). However, bats 1305 and 1314 had a common sibling, 1320, suggesting that they were siblings as well. Thus, we decided to assign a total of 3 paternal sibships in this group, confirming that 3 of the 4 young present in that group were sired by the same male (Fig. 5).

**DISCUSSION**

The results of our field observations suggest that *A. watsoni* exhibits a social and mating system characterized by mixed-sex, female-biased breeding groups with no (or nonexclusive)

**TABLE 2.**—Number of roosting groups of *Artibeus watsoni* in Golfito and Corcovado, southwestern Costa Rica, for which genetic analyses of parentage were conducted. These groups were composed of 1–4 young in groups either with no adult males or with 1 adult male.

	No. young			
	1	2	3	4
With 0 males				
Golfito	0	4	1	1
Corcovado	0	3	2	0
With 1 male				
Golfito	9	4	1	0
Corcovado	13	6	0	0

mating bonds. Males associated intermittently with females that frequently switched roosts, and access to females seemed to be related to the defense of roosts or roosting territories, because no male–male associations were observed at sites where females were present. Similarly, the results of the genetic analysis support the hypothesis of a mating system with female-biased, mixed-sex breeding groups in which males do not have exclusive mating access to these groups. For example, the fact that only 27% of young were sired by the male within a roosting group demonstrates the lack of mating bonds because, only 3 months after copulation, females were seldom found with the male who fathered her young. In addition, the fact that only 11% of young dyads roosting together were assigned as a paternal sibship, and the observation that female–female association indices were low, suggests that females roosting together during estrus did not maintain these bonds through parturition, and that no single male was able to monopolize copulations within social groups. However, our finding paternal sibships indicates that a few males were able to copulate with several females who were found together later during the parturition period, which is likely the result of a female-biased sex ratio of social groups, or the result of some males holding better roosting territories that give them access to more mating partners, or both.

The mixed-sex social groups with high roosting-group lability found in *A. watsoni*, coupled with absence of mating bonds and a low variance in male mating success, suggest that *A. watsoni* exhibits a mating system where both males and females have multiple mating partners. However, these mating partners seem to have long-term relationships because individuals associated with the same group members, continuously or intermittently, for several months despite frequent movement among roosts. Mating systems in which males and females mate with different individuals in successive mating attempts include polygamy (i.e., polygyny and polyandry) and promiscuity (Clutton-Brock 1989). However, promiscuous mating systems are found in species where individuals have no continuing relationships before or after mating, which is not the case in *A. watsoni*. Thus, *A. watsoni* seems to have a mating system characterized by a mixture of polygyny and polyandry, which is often referred to as polygynandry (2 or several males sharing access to 2 or several females, and vice versa—Davies and Lundberg 1984).

Mating relationships in which both males and females have multiple mating partners seem to be common among mammals, even among species that are socially monogamous (e.g., Goossens et al. 1998; Martin et al. 2007; Munshi-South 2007; Sillero-Zubiri et al. 1996). Within Chiroptera, there are also species that are socially or genetically, or both, polygamous or promiscuous. For example, it has been suggested that the leaf-roosting banana bat (*Neoromicia nanus*) has a promiscuous mating system given its labile social group composition, where males roost with multiple females and females roost with multiple males (Happold and Happold 1996). Vampire bats (*Desmodus rotundus*) form groups of several adult males and females, in which females preferentially, but not exclusively, copulate with males positioned at the top of the roost (Wilkinson 1985). Other species for which a polygynous mating system has been suggested even though paternity is not assigned exclusively to the dominant, or harem, male include *Artibeus jamaicensis*, *Rhinolophus ferrumequinum*, and *Saccopteryx bilineata* (Heckel and von Helversen 2002; Heckel et al. 1999; Ortega et al. 2003; Rossiter et al. 2000). Moreover, given that sperm competition is likely to be an important

**TABLE 3.**—Summary statistics generated by program CERVUS for *Artibeus watsoni* in Costa Rica for all 6 loci at the 2 sites, Golfito (G) and Corcovado (C), including number of alleles ( $N_A$ ), observed ( $H_O$ ) and expected ( $H_E$ ) heterozygosities, probability of exclusion when neither parent is known ( $P_{EX1}$ ) and when 1 parent is known ( $P_{EX2}$ ), and estimated null allele frequencies. Error rates for known parent–offspring mismatches also are included. Overall values represent means for number of alleles and heterozygosity, and overall values for the probabilities of exclusion are the products of individual values, assuming linkage equilibrium among loci. There were no significant deviations from Hardy–Weinberg equilibrium for any loci.

Locus	$N_A$		$H_O$		$H_E$		$P_{EX1}$		$P_{EX2}$		Null allele frequency		Error rate	
	G	C	G	C	G	C	G	C	G	C	G	C	G	C
AjA110	14	13	0.89	0.84	0.87	0.88	0.59	0.62	0.74	0.76	−0.0151	+0.0216	0.04	0.00
AjA47	13	13	0.96	0.86	0.87	0.88	0.59	0.60	0.74	0.75	−0.0515	+0.0105	0.00	0.07
AjA151	17	13	0.93	0.91	0.91	0.90	0.68	0.65	0.81	0.78	−0.0127	−0.0086	0.00	0.00
AjA40	16	13	0.77	0.81	0.90	0.88	0.65	0.60	0.79	0.75	+0.0786	+0.0417	0.07	0.03
AjA84	22	25	0.96	0.82	0.92	0.91	0.73	0.70	0.84	0.82	−0.0234	+0.0540	0.03	0.00
AjA123	15	14	0.86	0.89	0.87	0.88	0.59	0.61	0.74	0.76	+0.0065	−0.0052	0.00	0.00
Overall	16.16	15.17	0.89	0.85	0.89	0.89	0.9980	0.9976	0.9999	0.9998			0.02	0.01

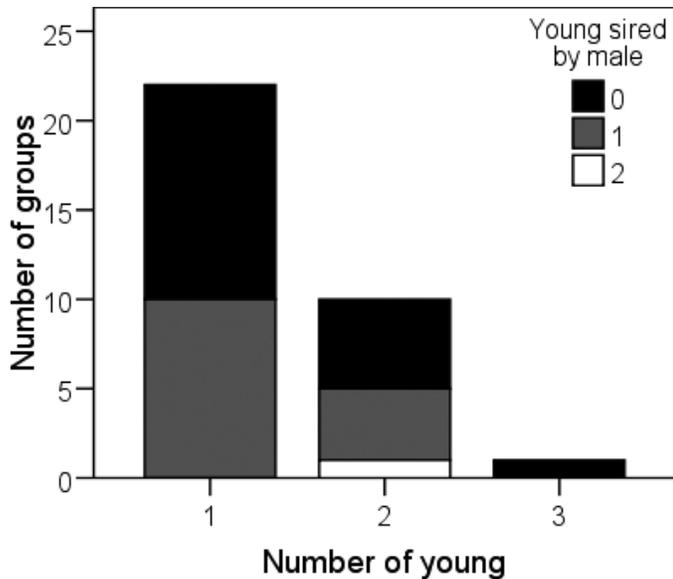


FIG. 4.—Number of groups of *Artibeus watsoni* composed of 1, 2, or 3 young that had 0, 1, or 2 young sired by the male captured with the roosting group.

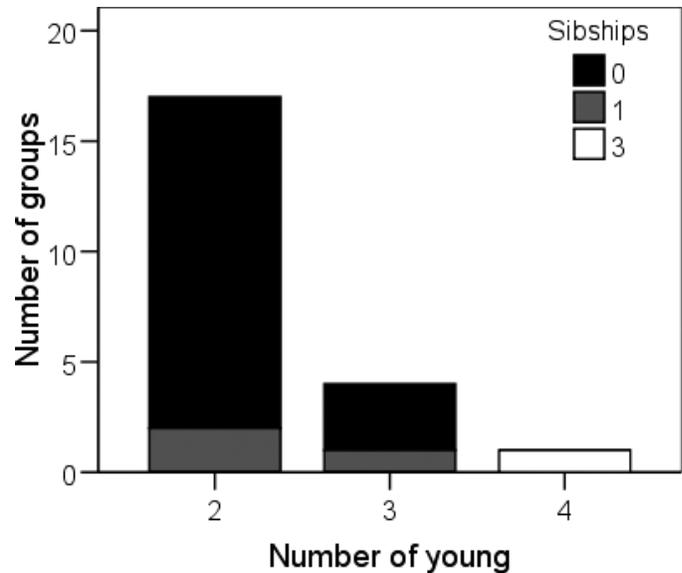


FIG. 5.—Number of groups of *Artibeus watsoni* composed of 2, 3, or 4 young that had 0, 1, or 3 paternal sibships (half-siblings with the same father).

phenomenon in bats (Hosken 1997), and that sperm competition occurs when females have  $>1$  mating partner within a period of sexual receptivity (Parker 1970), it follows that promiscuity and polygamy are probably more widespread in bats than previously thought.

Polygamous and promiscuous mating systems have costs to both males and females. For example, individuals may be prone to predation and incur energetic or time costs when searching for additional mating partners (Jennions and Petrie 2000), in addition to greater exposure to sexually transmitted diseases (Nunn et al. 2000). However, there are also obvious benefits to mating with multiple females (i.e., polygyny), because male reproductive success correlates directly with the number of females inseminated. Females also gain from having 2 or more mating partners (i.e., polyandry) through additive and nonadditive genetic quality of offspring, enhanced genetic variability among offspring, by insuring fertilization, and by securing parental care (Reichard et al. 2007). For example, it has been observed that female yellow-toothed caviies (*Galea musteloides*) paired with several males have more surviving offspring than females paired with only 1 male, presumably because of possible correlations between sperm success and offspring viability (Keil and Sachser 1998). Females from these species gain by having multiple mating partners, probably because they cannot reliably assess the genetic quality of males (Jennions and Petrie 2000).

Despite the benefits of having several mating partners for females, not all individuals and species mate multiply during the same reproductive season, indicating that there are species- and individual-specific characteristics that increase the chances of polyandry. Females are predicted to gain more from mating with multiple males when a small number of males have exclusive access to resources that are essential for reproduction, when males may become sperm depleted or when there is high

incidence of sperm-egg incompatibility, when there is no paternal care, when offspring genetic variability is advantageous, and when females cannot share fertilizations among males (Reichard et al. 2007). Given that males of *A. watsoni* seem to have no role in the care of offspring, that females cannot share fertilizations among males, and that females engage in reproductive activities such as mating, parturition, and lactation exclusively at the tent-roosts (Chaverri and Kunz 2006a), which are located within the territories of a few males, then having several male partners seems advantageous to females in this species. In particular, females of *A. watsoni* may gain directly by selecting several male partners whose roosting territories vary temporally in quality, and indirectly by copulating with males whose gametes may ensure offspring survival and whose offspring will have a greater reproductive success.

Resource-defense polygyny, defined as a mating system in which males gain access to several females by defending resources that are essential to them (Emlen and Oring 1977), is considered the prevailing mating system in tent-roosting bats. Most species sampled thus far have a harem-like roosting group composition in which single males roost with multiple females, and where males are thought to defend tents or roosting territories to gain access to breeding females (Campbell et al. 2006; Kunz and McCracken 1996; Storz et al. 2000; Tan et al. 1997, 1999). Thus, our study is the 1st to show a polygynandrous mating system with absence of exclusive mating bonds and low group stability in a tent-making bat. Unfortunately, many of the studies addressing the social organization and mating system of tent-making bats have not collected data on short- and long-term group stability, and only 1 has used genetic tools to understand mating patterns. Storz et al. (2001) addressed patterns of parentage in the harem-forming Old World tent-making bat *Cynopterus sphinx* and found a high variance in male mating success, with resident males siring most

offspring. However, Storz et al. (2001) did not address whether males sired most offspring within their harems, and also did not measure daily group stability. Another study on the Old World tent-making species *Cynopterus brachyotis* found substantial differences in the degree of daily movements of females among harem males, with strong harem fidelity in *C. brachyotis* Forest and female group lability in *C. brachyotis* Sunda (Campbell et al. 2006). Unfortunately, genetic data on patterns of parentage were not collected in that study. Thus, although these studies provide an essential 1st step to understand the mating system of tent-making bats, it is difficult to confirm polygyny in these species without data on mating success of harem males and the length and strength of mating bonds.

Even though there is sufficient evidence gathered to date that explains the ecological correlates of broad mating system categories (for example polygyny compared to monogamy, and resource-defense compared to female-defense polygyny), few studies have attempted to examine the causes of inter- and intraspecific variation within these categories in bats (e.g., Chaverri and Kunz 2006b; Chaverri et al. 2007b; Storz et al. 2001). Our study provides some preliminary evidence that suggests variation in the strength of association between our 2 main study populations in addition to spatial differences in male reproductive success demonstrated by the presence of paternal sibships in Golfito and their absence in Corcovado. The variation in the strength of association among sites is probably explained by the differences in the abundance of roosting resources, because tents are scarcer at Golfito in spite of populations being larger (Chaverri and Kunz 2006b). This lower availability of roosts causes clumping of individuals at a few tents, generating larger roosting groups and greater roost fidelity (Chaverri and Kunz 2006b; Chaverri et al. 2007b). If the number of females a male is able to roost with on any given day is greater in Golfito, and if female groups are more stable, it follows that a few males will be able to secure exclusive mating opportunities with more females in Golfito, causing greater male reproductive success, as suggested by the presence of paternal sibships in Golfito but not in Corcovado. Other studies also have observed a positive correlation among population density or clumping at roosts and variance in male mating success (Charmantier and Perret 2004; Hughes 1998; Pemberton et al. 1999; Storz et al. 2001). In addition, *A. watsoni* also exhibits significant roosting home-range size differences correlating with the abundance of roosts, and individuals in areas of high roost abundance have larger roosting home ranges (Chaverri et al. 2007c). Studies on dunnocks (*Prunella modularis*) have shown that the ability of males to secure exclusive mating opportunities depends on the size of females' ranges, with lower male mating success where females range over larger areas (Davies and Lundberg 1984). Thus, the presence of paternal sibships in Golfito also may be explained by the smaller home ranges occupied by females due to the scarcity of roosting resources. Finally, female bats also are more likely to mate with multiple males when they switch roosts often (Wilkinson and McCracken 2003), and so the greater roost fidelity expressed by females in Golfito generates fewer male partners at this site and a greater variance in male mating success.

In conclusion, our study shows that the tent-making bat *A. watsoni* exhibits a polygynandrous mating system with mixed-sex, female-biased breeding groups with nonexclusive mating bonds. Social group composition was very unstable, and males associated intermittently with females that frequently switched roosts. We also found spatial variation in patterns of association and male mating success, which, along with evidence from other studies, demonstrates that intraspecific variation in mating tactics is widespread and that individuals should adjust their behavior according to the environmental conditions encountered in their habitats. Finally, although our study is the 1st to describe a polygynandrous mating system in a tent-making bat, the paucity of detailed social and genetic data has precluded a thorough understanding of mating systems in these and other bats. Collecting these data will allow us to identify the social and genetic mating system of bats, helping to formulate appropriate theories regarding the evolution of social behavior in these mammals.

## RESUMEN

Los sistemas de apareamiento de los vertebrados son influenciados por factores ecológicos y filogenéticos, y la variación observada en el comportamiento reproductivo es atribuido con frecuencia al grado en el que el macho es requerido por la hembra para criar exitosamente a las crías, el tamaño y la estabilidad de los grupos de hembras, y la densidad y distribución espacial de las hembras. Como parte de una edición especial del *Journal of Mammalogy* originado del simposio de sistemas de apareamiento de la XIV International Bat Research Conference en Mérida, México, describimos el sistema de apareamiento del murciélago constructor de tiendas *Artibeus watsoni*. Durante 16 meses consecutivos muestreamos dos sitios en el suroeste de Costa Rica, determinamos el tamaño, composición y estabilidad de grupos sociales, y establecimos paternidad de machos en las tiendas. Encontramos que los grupos sociales están compuestos de algunos machos y muchas hembras localizados en varios refugios dispersos en un área. La asociación en los refugios era débil (promedio de 31%), y los cambios constantes entre miembros de grupos sugiere que esta especie forma parejas reproductivas no exclusivas, hipótesis reforzada por el hecho de que sólo el 27% de los juveniles fue engendrado por el macho en el refugio. También se encontró que el 17% de parejas de crías fueron engendradas por un mismo padre, lo que indica que pocos machos copularon con más de una hembra durante la época de apareamiento. Sin embargo, sólo se observaron hermanos paternos en Golfito, lo que se podría explicar por el mayor tamaño y estabilidad grupal atribuida a una menor abundancia de refugios. Por lo tanto, nuestros hallazgos son consistentes con un sistema de apareamiento poliginandro (2 o más machos tienen acceso a 2 o más hembras, y viceversa), donde los machos se asocian intermitentemente con hembras que constantemente cambian de refugio, y donde el éxito reproductivo de los machos parece depender de la defensa de refugios.

## ACKNOWLEDGMENTS

We thank P. Campbell and M. D. Sorenson for comments on earlier versions of the manuscript, and M. Gamba, O. E. Quirós, 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.

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*Special Feature Editor was Christian C. Voigt.*