**ORIGINAL PAPER**

# Hanging out in tents: social structure, group stability, male behavior, and their implications for the mating system of *Ectophylla alba* (Chiroptera: Phyllostomidae)

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## Abstract

Bats show the greatest variety of mating strategies in mammals. Social structure can be influenced by roost characteristics, for example, if the roost is defendable and its availability limited, it becomes an important resource that partially determines the mating system type. In the species that use tents as roosting sites, it has been suggested that males can defend the tent in order to attract and have access to females. *Ectophylla alba* is an obligate and exclusive tent user, and it has to build tents periodically. Its mating system has been classified as polygyny by its resource defense, and it has a temporary group structure of one male and several females. This study seeks to determine the composition and stability of the groups of this species and to learn whether males defend the tent or the females in it in order to gain copulations. This study was conducted in 2006 in Tirimbina, Biological Reserve in Sarapiquí, Costa Rica, where groups of bats were captured ($N = 38$). The individuals were marked ($N = 98$), and their reproductive status was determined. The behavior of the individuals was recorded with video cameras and infrared light (300 h total). Throughout the year, some individuals were more closely associated to other individuals, determining that groups are stable independent of the reproductive season. The proportion of males in the groups does not vary according to reproductive season, and in most groups, there is more than one adult male. The males spend different amounts of time in the tents and do not show antagonistic behavior with other members of the group. Based on the social structure, the classification of the mating system should change to "a stable group of several males and females," which may be confirmed in the near future by the results of an ongoing paternity study.

## Introduction

Bats are the group of mammals that present the widest variety of mating strategies (Altringham 1998). There are promiscuous species like *Myotis lucifugus* (Thomas et al. 1979) and monogamous ones, such as *Vampyrum spectrum* (Vehrencamp et al. 1977). There are also species with female defense polygyny in *Phyllostomus hastatus* (McCracken and Bradbury 1981) and *Pipistrellus kuhli* (Barak and Yom-Tov 1991), polygyny for resource defense as seen in *Artibeus jamaicensis* (Ortega and Arita 1999) and *Desmodus rotundus* (Wilkinson 1985), and leks (gathering of males competing for females) present in *Hypsignathus monstrosus* (Bradbury 1977a).

The understanding of these systems is far from being complete for most bat species, as their nocturnal and cryptic habits cause any research produced in the field to be difficult (Kerth 2008). According to McCracken and Wilkinson (2000), to date, there is only partial information about mating systems in only 7% of bat species. In any case, there is no other group of mammals with more diverse mating systems (Altringham 1998).

Given the relevance of the roost in the life history of bats, it has been pointed out that events associated to roosting sites

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can be an important factor to explain the social behavior of bats (Kunz and Lumsden 2003, Vonhof et al. 2004, Chaverri et al. 2007a, Kerth 2008). This social structure can be influenced by characteristics of the roost. For example, if the roost is limited and defendable, it becomes an important resource that can determine the mating system, where an individual (most commonly a male) monopolizes the resource and gains copulation access to females (Emlen and Oring 1977).

McCracken and Wilkinson (2000) proposed a mating system classification, based on the work by Bradbury (1977b), and organized the species according to their social structure in the roost site. As a result, knowledge of roost ecology is fundamental to understand mating systems of bats.

Worldwide only 24 species of bats (less than 2% of the total) are known that can modify the environment and build their own roosts. Of those, only 22 utilize leaves of tropical plants modified to be used as roosts, which are known as "tents" (Kunz et al. 1994, Rodríguez-Herrera et al. 2007). It has been suggested that species using tents have a polygyny mating system based on the defense of the resource (the tent) (Brooke 1990, Kunz et al. 1994, Balasingh et al. 1995, Kunz and McCracken 1996, Storz et al. 2000, Kunz and Lumsden 2003, Chaverri and Kunz 2006). The accepted assumed idea was that males build tents, and females select the male based on characteristics of the tents and his ability to defend the tent from other males (Balasingh et al. 1995, Kunz and McCracken 1996, Kunz and Lumsden 2003). However, Rodríguez-Herrera et al. (2006, 2011) published the first direct observation of a tent construction from a Neotropical bat, *Ectophylla alba*. Their results do not support the belief that just males build tents, as they documented that both sexes participate in the construction of the tents. It is clear then, that at least in this species, tent construction cannot be interpreted as a direct sign that females use it to select the male for mating, in case females effectively select a male.

*E. alba* is white, weighs between 6 and 9 g, and is endemic to a small region in Central America (LaVal and Rodríguez-H 2002, Simmons 2005). This species only roosts in tents, and the building process requires several nights of work (Rodríguez-Herrera et al. 2006, 2011) and very specific requirements for the microhabitat (Rodríguez-Herrera et al. 2008).

The first objective of this study was to determine the composition and stability of *E. alba* groups. Bats of this species must move to a new tent periodically when the tent reaches its useful life, which could imply the disbandment of the group. However, given the cost of finding a suitable leaf to modify as a new tent, and given the fact that several individuals of both sexes participate in the construction (Rodríguez-Herrera et al. 2006, 2011), the hypothesis was that the composition of the groups (individuals that share a roost) was stable through time, and the association between individuals could not be random each time they change roosts. The second objective was to test

the proposed hypothesis that the mating system of this species was one male with several females as has been stated by Brooke (1990), in which the male will defend the tent or the females gaining direct access to copulate with them (Kunz and McCracken 1996).

## Methods

### Study area

The study was conducted from July 2005 to December 2007 in Tirimbina Biological Reserve in Sarapiquí, Heredia province, Costa Rica (10° 24' N, 84° 07' W). The annual average of precipitation is 3900 mm (McDade and Hartshorn 1994), the altitude is 150 masl, and the life zone is tropical rainforest (Holdridge 1967).

### Data collection

From August 2005 through August 2006, groups of *E. alba* were captured in their tents during the day. A horizontal trap with a mosquito net was used, which does not damage the tent or the bats, and allows the capture of the whole group at each tent.

Data taken from each individual included: weight, sex, reproductive status, and forearm length, in addition to wing tissue for future studies to determine the kinship of the individuals. Each individual was marked with numbered metallic bands of 2.9 mm (Porzana Ltd), put in the left forearm in males and right forearm in females.

### Bat activity

For this specific objective, we chose a group with an accessible tent to film overnight from 17:30 to 05:30 with a Sony HandyCam DCR-HC42 camera and IRLamp6 model infrared lights (Wildlife Engineering) from a distance of between 0.75 and 1.25 m from the tent. The group filmed was composed of two males (♂1 and ♂2) and three females (♀1, ♀2 and ♀3). Pups after 2 weeks looked like subadults. During the course of the study, each female had a single pup, but one of the females (♀3) disappeared from the group. Given that individuals were marked with metallic bands, using the location of the band along the forearm (position near the wrist and left or right forearm) and for some noticed individual characteristics through the study, we were able to recognize each individual.

Film dates were classified in three periods: (I) (29 days previous to the birth of pups) eight nights, (II) (25 days after the pups are born until they are able to fly) nine nights, and (III) (up to 1 month after juveniles are able to fly) eight nights.

For each filming night, we quantified (1) the time that the male and the female were in the tent during the night and (2)

the number of times that each individual came back to the roost. Moreover, we recorded the interactions of each male toward the other individuals of the group.

## Statistical analysis

For describing the level of association between the individuals, we used the simple proportion index (see Cairns and Schwager 1987). For determining if there was a preference of association between individuals, we used the permutations method of Bejder et al. (1998) with the modifications proposed by Whitehead (2005). This method compares the index matrix of associations against the null hypothesis that individuals are randomly associated. When the deviation or the coefficient of variation are significantly greater than what is expected at random, then there is evidence that some individuals associate more with each other than with others. If the average of the association excluding zeros is higher, that means that associations are long-term in time. The matrix was made with 10,000 random permutations, and the analysis was performed in the SocProg program.

To analyze if the proportion of males in the groups changes between reproductive periods (as indicated by enlarged testicles) and the season when they were not reproducing, we applied a $t$ test.

We used an ANOVA of Friedman to discover if there were significant statistical differences in the time that individuals invest in the roost and the number of times that came back to it.

## Results

A total of 38 groups of *E. alba* were captured, with a total of 98 individuals marked. From those individuals, 44 were adult males, 6 subadult males and 48 adult females. No subadult female was captured. Some of those individuals were captured several times during the year of the study. All individuals were always captured and recaptured in their roost within approximately 12 ha. Recording of bat activity for each period was 96 hours in period I, 108 period in II, and 96 in period III, for a 300 h in total.

## Group structure

Average group size was 5.6 bats (2.45 SD). There was one group with a single individual and the largest group contained 11 animals. Groups were stable through time, and they maintained partnerships with individuals in the same group more than with other individuals at random. The level of association could be observed in the sociogram, where it was clear that some individuals associate more strongly with certain individuals than with others (Fig. 1). Of the 38 groups captured, 75%

had more than one male (Fig. 2). There were no statistical differences in the proportion of males in the groups throughout the year, and it appeared to be independent of the reproductive season ($t = 1.20$, $P = 0.24$, $df = 36$).

## Bat activity

Depending on the season, both males filmed from the group spent a different amount of time in the roost, and they also differed in the number of times that each male went back to the roost during the night. Unlike males, females spent a similar amount of time at the roost and also went back a similar number of times (Table 1). In the first period, ♂2 spent more time in the roost than other members of the group, including ♂1 [(Friedman ANOVA chi-square ($N = 8$, $df = 4$) = 10.239; $P < 0.03659$]. In this period, both males visited the roost more times than the females, Friedman ANOVA chi-square ($N = 8$, $df = 4$) = 14.347; ($P < 0.00627$), which implies that visits of ♂ 1 were shorter than of ♂ 2.

In period II, three of the females spent more time at night in the roost than in period I [Friedman ANOVA chi-square ($N = 9$, $df = 4$) = 28.607; ($P < 0.00001$)]. In this period, ♂2 came back more times to the roost each night than ♂1 and the three females [Friedman ANOVA chi-square ($N = 9$, $df = 4$) = 18.143; ($P < 0.00116$)].

In period III, there were no significant differences in the time that the members of the group spent in the roost [Friedman ANOVA chi-square ($N = 8$, $df = 3$) = 3.750 ($P < 0.28976$)]. However, ♂2 came back fewer times during the night than ♂1 and the three females, which implies that his visits to the roost are longer than ♂1.

Individuals from other groups did not visit the tent, which means that only the five individuals originally marked as members of that group, used the roost during the filming period. Males did not show agonistic behavior in any period.

The only interaction between males with other individuals was to bite and hold the central part of the back of another individual with the teeth without hurting them, visibly causing any pain, or the bitten individual attempting to be released from the hold. Only the males showed this behavior, especially toward females, although a couple of times males bit each other. That behavior was also present in subadult males over females, but never towards their own mother.

At the same time as biting, the male produces some kind of fast vibration with his forearms. The duration of this behavior varied from seconds to more than 5 min. Most often, the back of the bitten individual was left wet with the saliva of the male that was biting. This behavior did not affect the behavior of the individual being "bitten," i.e., if they were grooming, they kept doing it even if they were being "bitten" by the males.

**Fig. 1** Sociogram showing associations among 98 individuals during the study year. The width of the line means the degree of association between individuals (more width = the association is stronger)
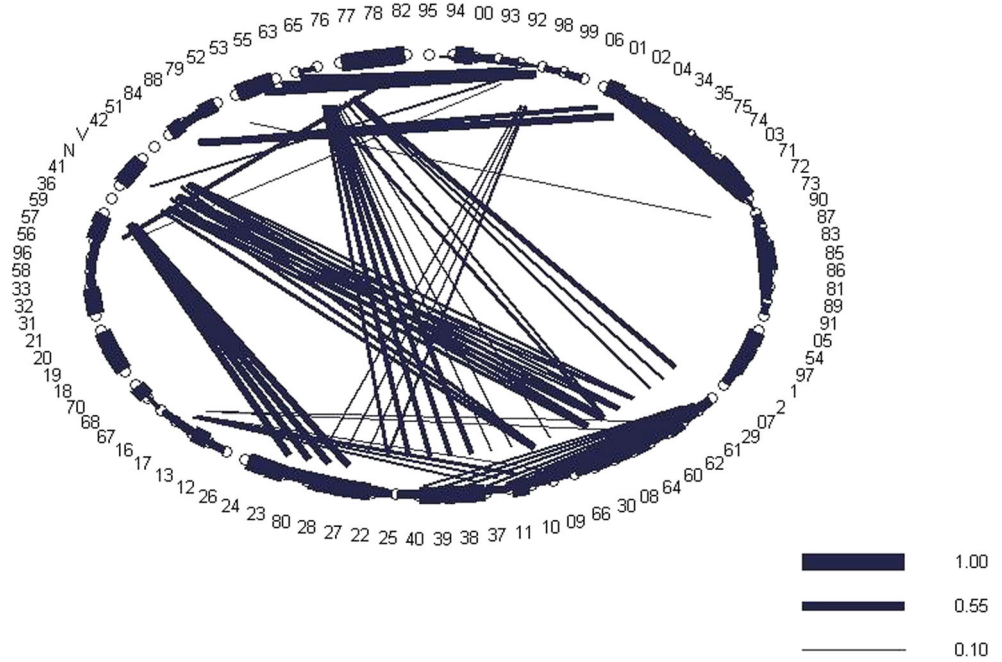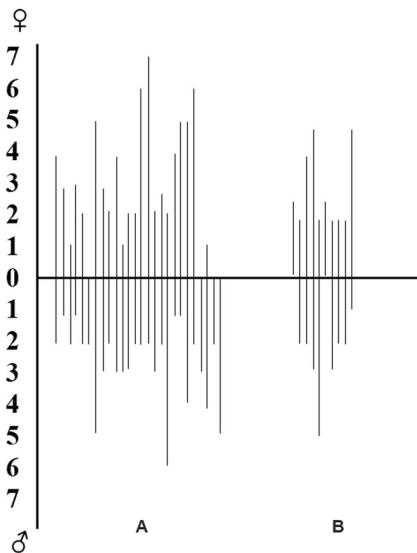


## Discussion

### Group structure

*E. alba* usually builds a new roost near the previous one (< 500 m; Brooke 1990, Rodríguez-Herrera et al. 2011). This implies that individuals remain within a relatively small area for at least a while. This behavior increases the number of encounters among the 98 individuals, and if the



**Fig. 2** Number of adult females and males (excluding offspring) of each group (each line represents a group), captured during the time of non-breeding (**a**) and breeding season (**b**)

species does not have a very stable, durable structure, it would stimulate the creation of new and different combinations of individuals into groups with a structure different from the original.

In spite of that, our results support the hypothesis that groups are very stable and long-lasting, and they do not disintegrate. Furthermore, there is a greater association between some individuals than with others. Most individuals stayed as part of a stable group throughout the study, with the exception of a few individuals of both sexes that changed group. There is evidence about stability in bats, for example, *Myotis bechsteinii* is a species that maintains social stability for more than 5 years, where fission-fusion dynamics are present, and this social structure is complex, such as those present in other species of mammals, such as elephants, dolphins, and primates (Kerth et al. 2011).

Group stability has been highlighted to be a demographic characteristic that promotes bat socialization (Emlen 1994, Kerth 2008). In *Artibeus watsoni*, which also uses tents, individuals are not randomly associated. However, the temporary stability of the groups of *A. watsoni* is lower and depends on the number of available tents, i.e., when tent availability is lower, groups are more stable, but when availability increases, the stability of the groups decreases (Chaverri et al. 2007b).

*A. watsoni* can use more than 40 species of plants to build their roosts, unlike *E. alba*, that uses mainly two plant species, and the process of habitat selection for roost construction is highly specialized to a certain stage of secondary succession (Rodríguez-Herrera et al. 2008). Some of the tents that *A.*

**Table 1** Average of time in the roost and average number of times that each individual came back to the roost during the night (I = 29 days previous to the birth of pups; II = 25 days after the pups are born until they are able to fly; III = up to one month after juveniles are able to fly)

| Individual | Time in the roost by night (minutes) | | | Number of times that came back to the roost during the night | | |
|---|---|---|---|---|---|---|
| | I | II | III | I | II | III |
| ♂1 | 112 (18) | 90 (18) | 197 (46) | 1.75 (1.5) | 1.2 (0.8) | 3.2 (1.4) |
| ♂2 | 222 (57) | 97 (18) | 159 (31) | 1.75 (0.9) | 4.7 (1.2) | 1.2 (0.5) |
| ♀1 | 122 (18) | 294 (58) | 242 (56) | 0.5 (0.5) | 4.6 (1.9) | 4.2 (1.7) |
| ♀2 | 115 (21) | 278 (92) | 223 (70) | 0.25 (0.4) | 5.6 (1.8) | 3.1 (1.3) |
| ♀3 | 102 (28) | 244 (64) | – | 0.12 (0.3) | 4.7 (1.9) | – |

*watsoni* uses are understory palms of the genera *Asterogyne* and *Geonoma*. Given the sturdy nature of the leaves of these species, tents built on them can remain in good condition for more than a year, and the number of tents in good condition without use is greater than the occupied ones (Rodríguez-Herrera unpublished data). *E. alba*, on the other hand, builds tents that last less than 2 months, and they only build when new tents are needed. It is uncommon to find tents in good condition that are not in use (Rodríguez-Herrera et al. 2011).

Groups formed by *E. alba* are very stable in time. Individuals roost together until the tent deteriorates, and then they move together to a new tent. This happens independently of the reproductive season (Rodríguez-Herrera et al. 2011). We suggested two ecological characteristics of the roost can promote that kind of stable associations among individuals. The first one is the lifespan of the tent and the availability of suitable leaves. Tents used by *E. alba* are an ephemeral resource. They last 7.5 weeks on average before becoming damaged beyond a usable state, and at some point before that happens, bats must start looking for a new leaf and start modifying it (Rodríguez-Herrera et al. 2011). Searching for the leaf that exhibits all the characteristics that bats need is costly in flight time, sacrificed foraging time, and increased exposure of bats to predators. The cost can be high, considering that availability of leaves to be modified as a roost is limited spatiotemporally, i.e., 14 weeks after unfurling, the new leaves usually showed transverse cuts. These cuts are physical damage, possibly due to wind and/or branches falling on the leaves, but not related to the activities of bats (Rodríguez-Herrera et al. 2011). Moreover, the microhabitat where the tent is built is very specific (Rodríguez-Herrera et al. 2008). The costs can be lower if members of the group share in the building process, thus sharing the benefit that the tent provides. Who decides when and which leave to modify? It is a question with no answer yet.

The second factor that possibly promotes the stable associations among individuals is the direct costs of the construction. The construction process is slow, and several individuals participate (Rodríguez-Herrera et al. 2006), sometimes taking more than 3 weeks to finish one tent. Furthermore, several individuals of the group keep modifying the tent after inhabiting it (Rodríguez-Herrera et al. 2011). Similarly, the costs can be reduced if they are shared. The benefits of building tents will be higher than the costs, if the task is shared by the members of the group. Likely, this system would not work if associations among individuals were random. With unstable random associations, it would be difficult to control the participation in the construction and that all individuals share costs. Another reason is if the individuals change groups at random, the probability of finding other individuals at the same time with the need of building a tent could be very low. It is known that stable groups facilitate the evolution of cooperativeness (Emlen 1994).

Social relationships with other group members, and potential ways individuals garner information about their environment are aspects to explain the collective decision-making and fission-fusion dynamics (Sueur et al. 2011), for example, *Ectophylla* is a specialist that only feeds on *Ficus culubrinae*, which produces fruit on every individual plant around three times a year. Bats of the same group fly to the nearest tree with the best fruits (Villalobos-Chaves et al. 2017), so the bats need to find a tree with fruits in the same region. In addition to having to periodically find a leaf suitable for a roost, are two environmental situations that may promote the stability of the groups. Moreover, it is possible that these conditions demand a transfer of information between individuals, and staying in the same group is one way to get information.

If groups are stable, how do individuals disperse? From the 98 individuals captured and marked, six subadults (all males) were never recaptured. On one occasion, an adult male was alone in a deteriorated tent, was marked, and then it disappeared from the area and was recaptured days later 6 km to the east of that point. From these observations, apparently males seem to disperse. It has been suggested that male dispersal occurs to avoid competition among related males (Hamilton and May 1977).

The dynamics of the social structure reported for *E. alba* is that before births (April and September in Costa Rica), there are big groups that include several males and females, and when the babies are born, smaller groups are formed by one male and several females with their young ($N = 4$) (Brooke 1990), suggesting a postpartum estrus, where the male defends females from other males to copulate with them. Our

data do not support this observation, as 75% of the groups had more than one male and sex ratio did not vary throughout the reproductive season or even after it (Fig. 2). The stability of the groups and the number of males throughout the year, showed that no harems were formed (a single male with a group of females), i.e., the group that was filmed remained with two males more than 1 month before the young were born and several months after, and did not show changes in its structure before and after the young were born.

## Bat activity

The males of the group did not show agonistic behavior between them. However, there are differences of the time invested at the roost. ♂2 invested more time in the roost before the young were born, but both males visited the tent a similar amount of time at night, which means that male ♂1 made more short visits. In this period, females were investing time in foraging, probably related to the physiological demands of pregnancy.

When the young were born, ♂2 kept investing more time in the roost and returned more times than ♂1, investing a similar amount of time and number of visits to females in the roost. In this period, the females came back more times and spent more time in the roost to feed and groom the young. Approximately 4 weeks after birth, when young were able to fly and were less dependent on the females, females returned fewer times and spent less time in the roost, and ♂2 returned less and spent even less time than the rest of the group. Despite the long period of filming, during this period, we did not observe copulation; this species may copulate at a site different from the roost. At least during the study period, there was no evidence of any roost or female defense by males.

## Implications of group structure and bat activity for the mating system of *E. alba*

On the basis of the observed social structure, like in other species of bats, Brooke (1990) suggested that *E. alba*, with an observed social structure of one male and several females, had a mating system of resource defense polygyny (Brooke 1990). Our results do not support this: the social structure of the groups of *E. alba* is a *stable group of several males and several females*. Among the males of the group, there is no agonistic behavior.

Our result suggest that the mating system of *E. alba* may be similar to *A. jamaicensis*, with a dominant male, that could be ♂2, in the case of the filmed group and one or two subordinate males (Ortega et al. 2003). Future studies should document the relative reproductive success of males in each group. The mating behavior of both males must be recorded.

Although this is one of the first species studied in this aspect, studying the mating system of other species of bats using tents will yield crucial knowledge to understand the relation between roost ecology and the social structure of bats. Given the unique natural history of tent-roosting bats, they provide a fascinating and ideal model to understand the implications of a temporary, high-investment roost, such as tents on the mating system and social structure of bats. In addition, such a study would also help further understand the stability (or lack thereof) of the groups and the potential relevance of specific behaviors, such as the biting of the back. The study of social structure and mating systems in bats is only starting, and with the current available technology, we expect a much greater pace of advance in the near future.

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