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Ecological aspects of the tent building process by *Ectophylla alba* (Chiroptera: Phyllostomidae)

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Twenty-two species of bats worldwide are known to use modified leaves as their roost, known as ‘tents’. It has been suggested that the mating system of these species is resource-defense polygyny, with the presumably male-constructed tent serving as an attractant of females, but in *Ectophylla alba* a female was observed building a tent. The objectives of this work were to determine: 1) if both sexes build the tent; 2) if there is a relationship between number of tents and mating seasons and 3) the time availability of the *Heliconia* leaves that this species uses to make its roost as well as the effect of the bats on the plant. The study site was the Tirimbina Biological Reserve, Sarapiquí, Costa Rica. During 53 weeks, we censused the tents of *E. alba* in nine hectares. Construction of tents was filmed with a video camera and infrared lights. To measure the average life of the tents and the leaves that had not been modified, we marked leaves that were visited weekly to monitor for deterioration. Our results show that both females and males construct tents. Roost construction is costly in terms of time and effort, so the bats maximize the time spent occupying the tent. The modifications that the bats make to the leaves considerably reduce the lifetime of the leaves. This has implications for both the plant used and for the bats that build the tents.

Key words: tent-roosting bats, *Ectophylla alba*, tents, *Heliconia*

INTRODUCTION

Investment of significant amounts of time and energy in roost construction and maintenance is a common trait in mammals such as rodents and carnivores. Given that a refuge provides protection against the elements and predation, and is often a suitable place for breeding and rearing of offspring, there is often a close relationship between the quality of the roost and the reproductive success of the individual (Morrison and Morrison, 1981; Alcock, 2001; Dechmann *et al.*, 2005). In some cases, females are exclusively in charge of constructing the refuge. In other cases, males participate in the refuge construction and invest in parental care to maintain access to females (Dawkins, 1976).

Bats are among the most ecologically and taxonomically diverse groups of mammals. Their diversity extends to roosts, with species known to use caves, hollow tree trunks, crevices, spaces under rocks, buildings, rolled up leaves, and others (Rodríguez-Herrera *et al.*, 2007). In contrast to other mammals, most bats use pre-existing sites for their

roosts. A few species, however, have the ability to construct their own refuge (Kunz and Lumsden, 2003). Only 24 species of bats worldwide (2% of the total species) are believed to construct their own roost. Of these, 22 modify leaves of plants as roosts, which are known as ‘tents’. Seventeen of these species are Neotropical and belong to the family Phyllostomidae, while the rest are Palaeotropical (Kunz *et al.*, 1994; Rodríguez-Herrera *et al.*, 2007).

It has been suggested that the mating system in tent-making bat species is polygyny based on the defense of the tent resource (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 generally assumed hypothesis is that males make the tents and females select a male because of tent characteristics. Tent construction is also assumed to be a proxy for the male’s capability to defend themselves against other males (Balasingh *et al.*, 1995; Kunz and McCracken, 1996; Kunz and Lumsden, 2003). This idea has only been supported with observations on the flying fox *Cynopterus sphinx*.

Males of this species are responsible for tent construction; they defend it from other males and are subsequently selected by females (Balasingh *et al.*, 1995). The process of tent construction by Neotropical tent-making species had never been directly observed until recently when a female *Ectophylla alba* was videotaped while constructing a tent (Rodríguez-Herrera *et al.*, 2006). If the tent is used to attract the opposite sex to mate, we expect an increase in number of tents in reproductive season. It is important, therefore, to have a better understanding of the mating system of tent-roosting bats and to know whether tent construction plays a role in mate selection (Dechmann *et al.*, 2005).

Ectophylla alba is a 6–9 g white bat distributed in the lowlands of the southern Caribbean Coast of Honduras, Nicaragua, Costa Rica and northeastern Panama (LaVal and Rodríguez-H., 2002; Simmons, 2005). As far we know, this species solely roosts in tents made from seven species of plants that they modify into the shape of an inverted boat (Rodríguez-Herrera *et al.*, 2007). It has been suggested that *E. alba* has a postpartum estrus, in April and September (Brooke, 1990). Their mating system has been described as a solitary male with a group of females, but little else is known (McCracken and Wilkinson, 2000).

Most roosts are made in *Heliconia imbricata* and *H. pogonantha* (Timm and Mortimer, 1976; Brooke, 1990; Rodríguez-Herrera *et al.*, 2007). The roost microhabitat has been shown to be very specific (Rodríguez-Herrera *et al.*, 2008). Selection processes by these bats at different spatial scales make its already small distribution theoretically even more reduced. Ecological variables such as duration of the tent, the temporal availability of leaves to build tents, and the effect tents can have on the plant, have never been studied.

The goal of this work was to document ecological aspects of roost construction by *E. alba*. The following specific issues were addressed: 1) to determine if just females, or both sexes construct the roosts; 2) to assess if there is a relationship between number of tents and mating seasons; and, 3) to document the average time that a leaf can be used as a roost and the degree to which modification of the leaf into a tent affects its longevity.

MATERIALS AND METHODS

Study Area

The study was performed between July 2005 and December 2007 at the Tirimbina Biological Reserve, Sarapiquí, Heredia

Province, Costa Rica (10°24'N, 84°07'W). The average rainfall is 3900 mm (McDade and Hartshorn, 1994), the altitude is 150 m and the life zone is Tropical Wet Forest (Holdridge, 1967). The study site was located next to the Sarapiquí River, and consisted of 9 ha, divided into a 7 ha secondary forest and a 2 ha, 30 year old abandoned cacao plantation (*Theobroma cacao*).

Direct Observation of the Construction

In order to have detailed information about tent construction, including how it was made and who (i.e. sex) participated in its construction, complete groups of bats present in a tent were captured using a horizontal mosquito-netting trap that did not harm either the tent or the bats. All individual bats were marked with a metallic, numbered 2.9 mm band (Porzana Ltd). Females were marked on the right forearm and males on the left. The weight, sex, reproductive state, and length of forearm of each individual were recorded. A tissue sample of each individual was taken for ongoing molecular genetic studies.

As this species takes more than one night to construct the roost (Rodríguez-Herrera *et al.*, 2006), leaves were checked during the day to find any roost in the process of construction. When one was found, the length of the cuts and the angle of the leaf with respect to the ground were measured. To document the construction process the same night, the tent-in-construction was filmed from 17:00 until 05:30 of the next day with a Sony HandyCam camera DCR-HC42 and infrared lights model IRLamp6 (Wildlife Engineering) at a distance of 4 to 6 m from the leaf, focusing the image on the underside of the leaf, exactly where the bats are situated when they are using the tent.

Relationship Between Tent Construction and Mating Season

To determine whether density of tents is related to the mating seasons, the presence of *E. alba* tents were documented and counted weekly in the study site from July 2005 to August 2006 (53 weeks). Tents were classified as new (i.e. without damage), in good condition (i.e. more than half of the leaf blade was without damage), or dead (i.e. when more than half of the leaf blade was dry or deteriorating). These data were also used to measure the useful life of a tent and to estimate the frequency of new tent construction.

Temporal Availability of the Leaves to be Used by Bats and the Effect of the Construction on Leaf Longevity

To evaluate both the average period that a leaf is suitable to be modified by bats (that is, without any damage to the leaf blade) and the average lifetime of a leaf when it is not modified into a tent, 30 newly sprouted leaves were marked between February and April of 2006 in the study site. Leaves were checked weekly to document physical damage such as cuts to the leaf blade or damage caused by herbivores. In previous observations, we determined that bats do not choose to construct tents in leaves with previous damage.

To evaluate the effect of tent construction on the plant, the longevity of intact leaves and tents was compared using a *t*-test. Also we compared the longevity of each tent for an additional fourteen weeks against the longevity of the leaves. Fourteen weeks is the average ($n = 28$) amount of time that a leaf remains

in good condition for tent construction, so we assume that each tent was built with a leaf that had been opened for a maximum of 14 weeks.

RESULTS

Direct Observation of the Construction

A total of 98 individual bats in 36 groups (mean group size = 5) were captured and marked in the study site, including 44 adult males, 48 adult females and six subadult males. The number of individuals varied during the 53 weeks, but there were always at least two groups present.

We recorded 145.5 hours of video in 13 nights. In four tents and nights we managed to film individuals modifying the leaf for a few minutes. During most nights of filming, the bats did not arrive to the tent, or when they did, they did not modify the leaf. All the leaves that the bats started to modify had been open for only a few days, without damage to

the blade and with an angle of more than 45° to the ground. Furthermore, in these leaves one could observe lines of small holes from the edge of the leaf blade to the midrib. We assume that these small holes are the traces that the bats leave when they land on the edge of the leaf and then walk on the underside of the leaf to the midrib, where they start constructing the tent.

In all the observed and filmed constructions, the bats start the tent by modifying the leaf from underneath, first making holes with their teeth and then grabbing hold with their feet and thumbs and breaking some leaf fibers by pulling it downwards with their thumbs. This process creates the characteristic inverted boat shape (Fig. 1). The specific observations in different events is summarized as follows:

Tent A: On February 10th and 11th, a female and an unmarked individual arrived at the leaf without modifying it. This leaf was converted into a tent sometime between February 11th and 28th of 2006, but we did not record the process.



FIG. 1. Deterioration of the roost in 35 days, a — 28 February 2006, b — 21 March 2006, c — 30 March 2006, d — 05 April 2006, on this date was abandoned

Tent B: On February 28th we found a leaf of 97 cm length with two cuts on each side of the midrib (4.7 and 7.0 cm). On March 1st, after 20:00 hrs, after we stopped filming, the bats cut 12 cm from the center toward the base. On March 12th no bats arrived to the tent. March 14th the bats arrived and left without modifying the leaf. Between March 15th and 18th, the cut increased to 11 cm reaching the tip of the leaf and March 20th, 7 cm towards the base. March 21st around 18:20 two females and one male landed on the leaf, after which one female modified the leaf. A female was even modifying it while a male was present on the leaf. March 22nd the tent was occupied by five individuals. The tent was used until April 6th, on that date we captured the individuals and the tent was already in bad condition.

Tent C: On March 1st we found a leaf of 84 cm length with one cut (34 cm) parallel to the midrib. This night at 03:56 h a bat arrived and remained in the tent for nine minutes, making some perforations, and spending four minutes making holes that serve for landing as described in Rodríguez-Herrera *et al.* (2006). The bat was unmarked, thus we could not determine the sex. This tent was not occupied and construction was abandoned.

Tent D: On March 9th we found a leaf of 103 cm length with two cuts parallel to the midrib (18 cm each one). This night we filmed from 17:30 to 06:00 h, but no bats arrived. On the night of March 11th,

the cut was increased to 14 cm more towards the base of the leaf. On March 16th we filmed from 17:30 to 06:00 h but no individuals arrived. This tent was not occupied again.

Tent E: The leaf opened March 6th, and cuts (43 and 44 cm) parallel to the midrib were made sometime during five days before April 5th. That day we filmed from 17:30 to 05:30, but no individuals arrived. On April 12th we filmed (17:30 to 05:30 h) a female modifying the leaf for a few seconds. The tent was occupied from April 16th until June 15th.

Tent F: The tent was almost completed when we found it on September 20th. That night at 18:00 h, under heavy rains, a male arrived and groomed himself for 10 minutes, but did not modify the leaf. That same night at 04:23 h another male (we cannot ascertain whether it was the same one), groomed itself for two minutes and afterwards modified the leaf for five minutes making landing points while another individual flew over the leaf. The male groomed itself for another two minutes, worked on the leaf for two more minutes, and then left the tent. The tent was occupied for one day.

Relationship Between the Tent Construction and the Mating Season

Tent production rate remained constant throughout the year, with a new tent documented every 5–7 weeks (Fig. 2). The highest number of tents was

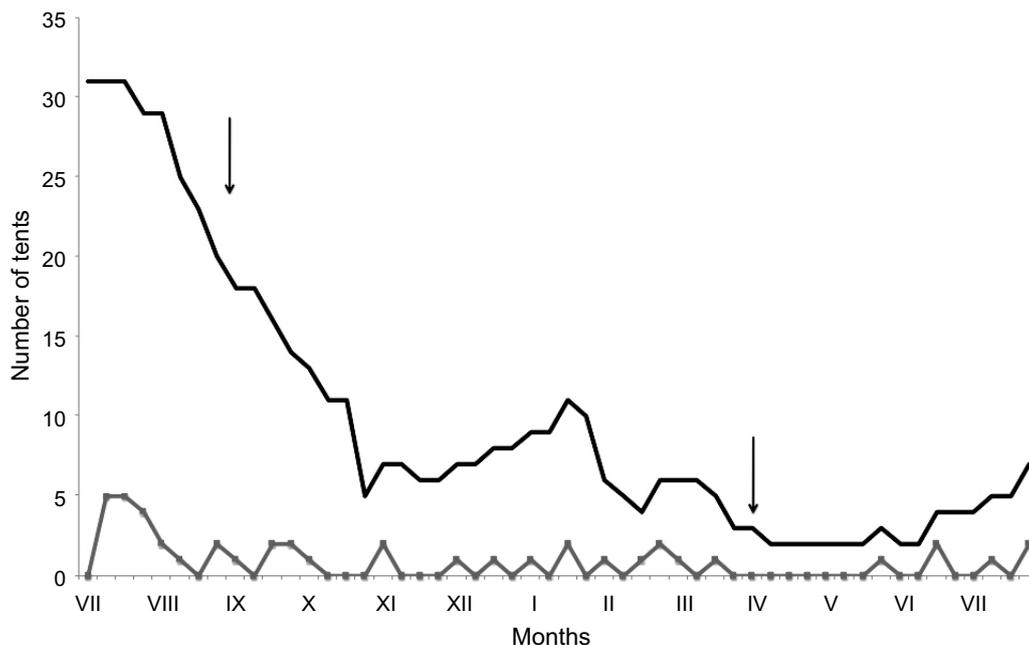


FIG. 2. Number of roosts built by bats weekly for a year, in 9 ha. The black line represents the total number of tents detected whereas the grey documents the presence of new tents. Arrows indicate the period of births

recorded in July, when the largest number of groups (6) was also recorded. During these weeks of assumed oestrus, no increase in tent production was observed.

Temporal Leaf Availability and the Effect of Leaf Modification on Leaf Longevity

On average, 14 ± 9.8 weeks ($n = 28$) after unfurling, unmodified 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. After a leaf suffers any type of physical damage it will not be used for tent-making by bats.

The modification of the leaf into a tent has a very strong negative effect on the average life of the leaf, probably causing an effect similar to heavy herbivory. The average life of a leaf that was modified as a tent was 7.5 ± 5.8 weeks ($n = 32$). This period was significantly different than the lifetime of an unmodified leaf, which lasted an average of 61 ± 32 weeks ($t = 9.28$, $d.f. = 58$, $P < 0.001$). In a more conservative analysis, we added the average age at which most leaves become damaged and were no longer an available resource for the bats to the tent longevity data (14 weeks). The duration of leaves used as tents and unmodified leaves was also significantly different ($t = 6.88$, $d.f. = 58$, $P < 0.001$).

DISCUSSION

Roost Construction and Implications on the Mating System

This is the first study to systematically document the building process of several tents and record that both sexes have the ability to modify the leaves. It is also the first to evaluate temporal availability of leaves to build tents and determine the duration of the roost and their effect on the plant.

The only previous observation of Neotropical bat tent construction was by Rodríguez-Herrera *et al.* (2006) who observed a female *E. alba* building a tent. Before that Muñoz-Romo and Herrera (2003) reported *Artibeus lituratus* making a leaf modification, but the leaf did not change shape as a result of behavior of bat, was not a tent. To our knowledge, prior to this investigation, only three species of bats in the world had been observed during roost construction. In two of them, only the males are responsible for the construction. In *Lophostoma silvicolium* (Phyllostomidae), the male

excavates the roost in termite nests of the species *Nasutitermes corniger*. Inside each active termite nest, the male forms groups with various subadult females or adults and juveniles; the male also defends the roost (Dechmann *et al.*, 2004, 2005; Dechmann and Kerth, 2008). Larger males are often more successful in forming and defending a group of females, with a reproductive success rate of 46% (Dechmann *et al.*, 2005). The flying fox *Cynopterus sphinx* (Pteropodidae) constructs tents by modifying the leaves of *Vernonia scandens* and *Polyalthia longifolia*. The male marks the tents with saliva and defends it from other males (Balasingh *et al.*, 1995). Much like in *L. silvicolium*, a group of females forms a harem, defended by the roost-constructing male (Dechmann and Kerth, 2008).

The mating system of *L. silvicolium* and *C. sphinx* has been classified as resource-defense polygyny based on the constructed roost. In general for tent-roosting bats, it has been suggested that the mating system is resource-defense polygyny, with the males presumably constructing the tent (Brooke, 1990; McCracken and Wilkinson, 2000).

We observed more than one individual involved in construction of the same tent and even after occupying the tent, different individuals of both sexes made modifications on different nights, improving the quality of the tent (B. Rodríguez-Herrera, unpublished data). Our observations demonstrate that both sexes participate in the construction and the tent is not a way for males to gain access to females.

The amount of time the bats invest in constructing the tent varies from a few nights to a few weeks, probably related to the number of individuals that participate in tent construction and the intensity with which the individuals work. Occasionally, many nights pass without modifications to the leaf. We assume that the intensity of the work effort depends on the urgency for the group to move to a new tent, but further investigation is needed to determine what prompts the group to build more quickly or with more help.

The videos showed that the construction process is probably costly and that the modification of the leaf is slow. Because the bats invest substantial effort, the roost must be highly valued and the bats may try to select roost location to maximize benefits derived from the roost. The roost is likely to provide benefits including protection against the weather (rain, solar radiation), and avoidance of parasites and predators (Timm, 1987; Kunz *et al.*, 1994). Bats appear to regularly build tents only when they need

them (Fig. 2); this can be explained by the high cost of construction.

Much remains to be discovered about the evolution of tent-making behavior and the cooperation among individuals to build tents in *E. alba* and other tent-making bat species. It is possible that the evolution of multiple individuals participating in tent construction may have arisen through kin selection, in that the group members are probably related and work together to share the costs and benefits of construction.

Until young *E. alba* are able to fly at 3–4 weeks of age, the mothers leave the young in the tent while they forage. It is therefore vital to have a secure place for the offspring. If the males in each tent are the fathers of the young, then tent building would directly benefit their reproductive fitness, assuming that tent-building increases the probability of survival for their young. If there is no relationship among the individuals of the group, roost construction by multiple individuals may be a cooperative behavior (see Clutton-Brock, 2002). The non-related individuals would receive direct benefits from the tent and would increase their long-term reproductive success. All members (at least the females) would have a net increase in reproductive success through the cooperative behavior. To fully understand the mating system of *E. alba* in an evolutionary context, it will be necessary to combine the data we collected on social structure and nocturnal roosting behavior with genetic information from the tissue samples we collected. Only then will it be possible to more accurately interpret the tent making behavior and the participation of both sexes and several individuals.

Temporal Leaf Availability and the Effect of Leaf Modification on Leaf Longevity

Roost fidelity, or the time a bat uses the same roost, has been hypothesized to be inversely proportional to the availability of the roost substrate (Lewis, 1995). For example, bats using caves do not abandon them quickly or easily because another cave with similar characteristics might not be available. Since tent roost plants may be fairly abundant locally, it has been hypothesized that tent-roosting species may be less loyal to their roost. Our census results show, however, that *E. alba* indeed has high tent roost fidelity compared to another tent-roosting bat, *Artibeus watsoni* (Chaverri and Kunz, 2006). We speculate that this is due not only to the high cost of constructing the tent, but also because tent plant resources are spatially and temporally limited for

E. alba. Although *Heliconia* is locally abundant, *E. alba* has very specific requirements in terms of leaf characteristics and micro-habitat (Rodríguez-Herrera *et al.*, 2008). The leaves must be less than 30 days old and measure between 0.8 and 1.2 m long (Brooke, 1990). The plants must be present in high canopy cover and in an understory that is clear between 0 to 1 m high, which implies a certain age secondary forest (Rodríguez-Herrera *et al.*, 2008). In contrast, *A. watsoni* used more than 40 species of plants from several families (Rodríguez-Herrera *et al.*, 2007).

All leaves used by the bats to construct new tents in this study were in perfect condition, with no transverse cuts or herbivory or damage to the leaf blade. After opening, the new leaves of *Heliconia* last, on average, only 14 weeks until damage occurs. The availability of leaves to be modified by bats is limited not only by their preference for a specific habitat (Rodríguez-Herrera *et al.*, 2008), but also by characteristics of the leaves themselves. The selection of leaves by the bats, by characteristics such as size, height and position has been documented in other species such as *Artibeus cinereus*, *A. watsoni*, *Uroderma bilobatum* (Timm and Lewis, 1991; Stoner, 2000; Machado *et al.*, 2008).

The specific conditions required by the bats increase the value of the tent-roost, which in turn favors or promotes roost fidelity in this species. During a year of census, we generally observed that bats only construct a new tent when more than 50% of the surface of the current tent has deteriorated (see Fig. 1d). Rarely do they abandon a tent in good condition. When this happens, it is probably because of a predation attempt that forces them to flee and change roost site. Predation at tent sites has been documented in various species of bats, including *E. alba* (Boinski and Timm, 1985; Rodríguez-Herrera *et al.*, 2007, 2008).

The average life of the leaves that *E. alba* uses for tent construction is reduced by 88% due to tent construction, causing a negative effect on the plant's fitness that remains to be quantified. The effect of tent construction can be especially costly to the plant if the bats use more than one leaf per plant, as has been commonly observed (B. Rodríguez-Herrera, personal observation). Cholewa *et al.* (2001) examined the vascular anatomy in the leaves of *H. pogonantha* to investigate whether the cuts themselves decrease the flow of water within the leaf blade, thus causing earlier mortality. They concluded that the leaves show a system of small transversal veins that maintain the water flow even with cuts, decreasing

the damaging effect to the leaf. The longevity reduction of 88% to modified leaves, however, happens despite this physiological adaptation. It would be worthwhile to further investigate how the reduction in leaf longevity is caused by the construction of a tent, and what effect this might have on the reproductive success of the plant.

Similarly, it is important to make more detailed observations to determine the composition of the groups that roost in tents, their level of kinship, their mating system, and the relationship they maintain with other nearby colonies. Studying behavior and mating systems of other tent-making bats will help understand the evolution of this unusual behavior and the variations and implications for the biology of bats. Likely, both behavioral and molecular genetic approaches will be crucial to fully understand this particular phenomenon.

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