Consistent individual positions within roosts in Spix's disc-winged bats

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ABBREVIATED TITLE: Consistent positions within bat roosts

ABSTRACT

Individuals within both moving and stationary groups arrange themselves in a predictable manner; for example, some individuals are consistently found at the front of the group or in the periphery and others in the center. Each position may be associated with various costs, such as greater exposure to predators, and benefits, such as preferential access to food. In social bats, we would expect a similar consistent arrangement for groups at roost-sites, which is where these mammals spend the largest portion of their lives. Here we study the relative position of individuals within a roost-site and establish if sex, age, and vocal behavior are associated with a given position. We focus on the highly cohesive and mobile social groups found in Spix's disc-winged bats (*Thyroptera tricolor*) given this species' use of a tubular roosting structure that forces individuals to be arranged linearly within its internal space. We obtained high scores for linearity measures, particularly for the top and bottom positions, indicating that bats position themselves in a predictable way despite constant roost-switching. We also found that sex and age were associated with the use of certain positions within the roost; for example, males and subadults tend to occupy the top part (near the roost's entrance) more often than expected by chance. Previous studies have shown that communally-roosting species often scramble to gain access to central positions, which are typically occupied by dominant individuals; thus, we speculate that our findings could also indicate some form of dominance hierarchy in our study species.

Keywords: Bats, dominance, linearity, Resource Holding Potential, roosts

LAY SUMMARY

Selecting an ideal position may be a critical decision for bats that roost inside developing tubular leaves. By tracking the position of disc-winged bats within their vertical roosts, we show that individuals are arranged linearly in a consistent manner. Our results suggest that dominance hierarchies might influence individual positions and hint at the existence of differential costs/benefits associated to each position.

INTRODUCTION

The relative spatial position of individuals within groups is relevant for understanding the consequences of social living, as this may determine vulnerability to predation and access to resources (Bumann et al., 1997; Morrell & Romey, 2008). For example, animals positioned at the front of a moving group need to invest more time in vigilance and are also subject to significant predation risks (Di Blanco & Hirsch, 2006; Dirk et al., 1997; van Schaik & van Noordwijk, 1989), but they may also have greater feeding success (Hirsch, 2011). For stationary groups, studies have shown that individuals are often positioned predictably either on the periphery or the center of the group, which could also affect predation rates (McGowan et al., 2006; Rayor & Uetz, 1990). What is common to both moving and stationary groups is that these risks and costs are highly influenced by site-specific conditions; for example, the risks faced or perceived by individuals in the periphery of groups may vary depending on a predator's attack distance and habitat structure (Hirsch & Morrell, 2011; Minias, 2014).

Many animals, most notably bats, spend a large portion of their lives within structures that they use for roosting. In these sites, individuals can avoid adverse environmental conditions and predators; they also conduct many important fitness-related activities, such as grooming, feeding, nursing, and copulating (Kunz, 1982). Roosts have heterogeneous internal conditions, and thus protection against predators and/or inclement weather is not equally distributed within them. Thus, we would expect that dominance relationships determine access to the best positions within a roost, as has been observed for stationary groups in other taxa. In colonial spiders (*Metepeira incrassata*), starlings (*Sturnus vulgaris*), and long-tailed tits (*Aegithalos caudatus*), it has been found that some individuals are typically positioned in the center of the group or colony, and that monopolization of these preferred locations is based on individuals' dominance

status (McGowan et al., 2006; Rayor & Uetz, 1990; Summers et al., 1987). However, despite the importance of roosts for the lives of bats, and the accumulated evidence of consistent differences in individual positions within both moving and stationary groups in other taxa, there are no studies yet that have addressed whether bats consistently select specific positions within their colonies while roosting.

Here we test whether Spix's disc-winged bats (*Thyroptera tricolor*) consistently select specific positions within their groups while roosting. This species lives in highly cohesive and relatively small groups of approximately 5-6 individuals (Chaverri & Gillam, 2016). We take advantage of two unique aspects of the natural history of *T. tricolor*: its use of a tubular roosting structure that seems to force groups to be arranged linearly within its internal space (Findley & Wilson, 1974), and the need to relocate daily to a new roost site. The latter occurs because the developing tubular leaves used as roost-sites open in approximately 24 hours (Vonhof & Fenton, 2004), which presumably forces group members to scramble for the best position within the new tube on a daily basis. While we provide no assessment of costs and benefits of different locations within the leaf's tubular structure, we explore how certain traits may be associated to specific positions. This will allow us to provide initial clues as to whether some form of dominance relationships mediate the selection of specific positions and develop new hypotheses to test in further studies.

In societies with linear hierarchies, it is often observed that a certain set of individuals dominates over other group members and thus can monopolize resources or ideal positions (Herrera & Macdonald, 1993; Wittig & Boesch, 2003). This effect is referred to as resource holding potential (RHP; Parker 1974; Taylor and Elwood 2003). In many taxa, RHP is associated with body size (Holand et al., 2004; Roden et al., 2005); therefore, if there is sexual dimorphism

in that trait, then a possibility is that the larger sex will also have greater RHP. Age is also associated with RHP, since adults typically dominate over juveniles or subadults (Holand et al., 2004; Lu et al., 2013; Roden et al., 2005). Therefore, in our study we predict that dominance over positions within the roost will be primarily assigned to females, which are larger than males (Chaverri et al., 2021), and adults. Since we have not assessed the costs and benefits of different positions within the roost, we cannot accurately predict which position will be dominated by individuals with potentially greater RHP. However, previous studies on colonially breeding birds show higher consistency of individuals occupying outer positions compared to inner ones, most likely since dominant individuals are constantly fighting for access to central positions while subordinate individuals are consistently relegated to the periphery (McGowan et al., 2006). Thus, we can predict that peripheral positions will be more stable while central ones will be more labile. Also, we predict that the bottom position will be primarily occupied by vocal bats, as previous studies suggest that the most vocal individuals are also the ones that first discover the roost site (Sagot et al., 2018). We assess vocal behavior based on whether individuals produce (vocal) or not (nonvocal) response calls, which are emitted by bats that have found a suitable roost site (Chaverri et al., 2010), and those calls promptly recruit other group members which presumably would position themselves above the bat that first located the roost.

METHODS

Data acquisition

We collected data on *T. tricolor* roosting behavior between November 2017 and May 2018 at Barú Biological Station in southwestern Costa Rica. We searched during the day for furled leaves to identify potential roosts, i.e., leaves which are occupied by a set of individuals (between 1-11, average = 5; Chaverri and Gillam 2016) considered to belong to the same social group. The population of *T. tricolor* in this area has been thoroughly studied (Chaverri et al., 2020) and many bats carry a PIT tag (Biomark Inc., Boise, USA) implanted subcutaneously in the mid-dorsal area. Each tag corresponds to a unique alphanumeric code and allows individual-level identification. On the first encounter, we trapped bats and installed PIT tags when missing (permit SINAC-ACOPAC-RES-INV-008-2017). In all subsequent encounters, we recorded the relative position of each individual within the tubular structure (**Figure 1**) by carefully scanning the leaf from top to bottom with an HPR Plus reader and custom-made antenna (Biomark Inc., Boise, USA). We recorded the sex and age of each bat. To test if vocal behavior is correlated to roosting position, we also analyzed the maximum number of response calls emitted by the same identified bats following methods used in previous studies (Chaverri et al., 2020).

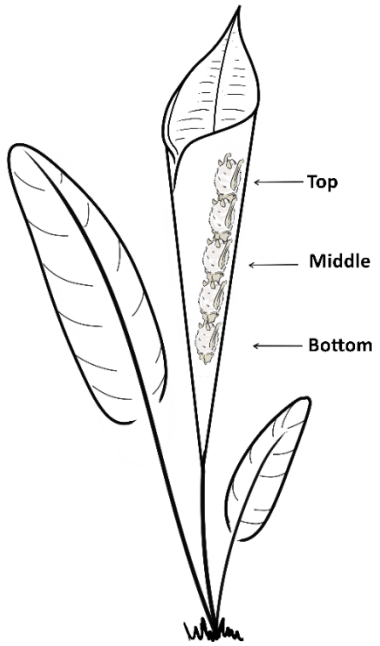

Figure 1. Drawing that shows how bats position themselves within the tubular leaf while roosting, and which individual was located at the top, middle, and bottom. Illustrated by Silvia Chaves-Ramírez.

Linearity and dominance

We were interested in estimating whether bats consistently positioned themselves in a specific order within the tubular leaf and thus obtained two measures: linearity and dominance. Linearity in our study would mean that, for example, bat *a* is always on top, bat *b* always goes second, bat *c* always goes third, and so on. Linearity was estimated using de Vries' (1995) *h'*, a modification of Landau's (1951) h, which measures the level of consistency in linearity and goes from 0 (each individual dominates exactly half the others) to 1 (a perfectly linear hierarchy). As we had no a priori expectation of which position would be dominant, we estimated linearity for all possible arrangements within the tubular structure: top to bottom, middle to bottom/top, and bottom to top.

Dominance was also calculated to determine which individual(s) were consistently found in a specific position within the tubular structure. For this we estimated David's (1987) score for each group member. The score produces large positive values for individuals that typically "dominate" (they are consistently found in the top, the middle, or the bottom) and large negative values for individuals that are "dominated". Again, as we had no a priori expectation of which position would be dominant, we calculated three dominance scores per individual: one assuming that the individual at the top is dominant, one where the middle is dominant, and one where the bottom is dominant.

To calculate linearity and dominance indices, we input the data in SOCPROG (Whitehead, 2009) in group mode allowing for interactions between all group members and for asymmetric interactions within the group. We organized the input data by collection date for each group with the unique bat codes ordered in each entry line. The software assumes that if bat *a* is the first of the sequence, it "dominates" over the other bats. Therefore, we arranged the data in three different formats in order to compute the indices considering 1) the top position as dominant (bats in order from top to bottom: *a, b, c, d, e*); 2) the bottom position as dominant (bats in order from the bottom to the top: *e, d, c, b, a*); 3) and the middle position as dominant (bats in order from the middle to the two extremes: *c, d* & *b* in random order, *e* & *a* in random order). For each group, we analyzed the three datasets separately.

Statistical analysis

We determined whether sex, age, and vocal behavior affected dominance (David's score) at particular positions within the tubular structure. For this we only considered the individuals with

the highest score within each group per position. We applied Bayesian binomial tests in the BayesianFirstAid R package (Bååth, 2014) to determine the probability of successes, i.e., instances in which females, adults or vocal bats dominated a given position (see predictions). We determined what proportion of the distribution of posterior probabilities was different from an expected distribution of values equal to the proportion of females (0.57), adults (0.75), and vocal bats (0.45) in the population (i.e., the subset of individuals that comprised our study, n = 37). Only 6 groups had individuals of both ages (adults and subadults), so we only considered these for the binomial test on age. For the effect of vocal behavior on dominance scores, we first categorized bats as either vocal (produced at least one response call) or non-vocal (produced no response calls). The beta prior was set to 1, and the results are based on 100000 iterations.

RESULTS

We collected data on the relative position of 37 individuals belonging to 10 groups of different sizes (two groups of five, three of four, and five of three individuals). We resampled each group 12.5 ± 6.2 times (mean ± standard deviation). Measures of linearity (de Vries' *h'*) were close to 1, indicating that bats consistently positioned themselves within the tubular leaf in a specific linear order. Linearity was greater and less variable when calculated from bottom to top positions and then from top to bottom, while the middle position was the most labile (**Figure**). The latter suggests that peripheral positions are more stable while central ones are unstable.

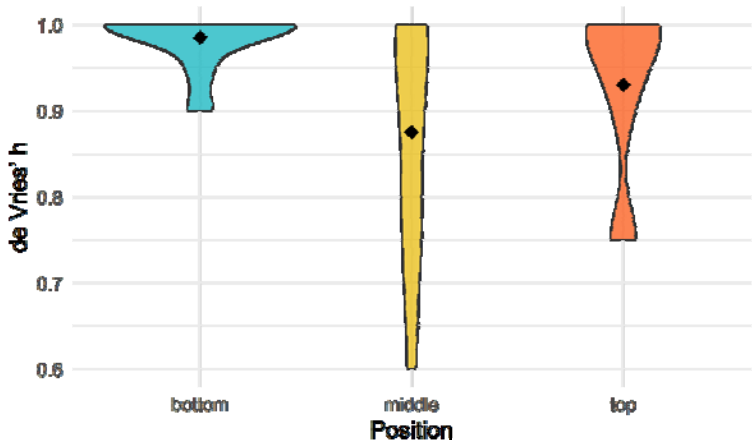

Figure 2. Violin plot of de Vries' *h'* by the position of dominance. The dot shows the mean for the position.

The dominance index (David's score) identified which individual(s) consistently occupied a specific position (top, middle, or bottom) within each group (**Supplementary Table 1**). Regarding sex, we found that the relative frequency of success for the top position is more than 0.57, the expected value under the null hypothesis, by a probability of 0.011 and less than 0.57 by a probability of 0.989. This indicates that males have a higher probability of occupying the top position (**Figure 3**). For age, we found that the relative frequency of success is more than 0.75, the expected value under the null hypothesis, by a probability of 0.013 and less than 0.75 by a probability of 0.987. This indicates that subadults are more likely to occupy the top position. Contrary to our initial prediction, we found no evidence to suggest that vocal bats were more likely to occupy the bottom position (**Figure 3**).

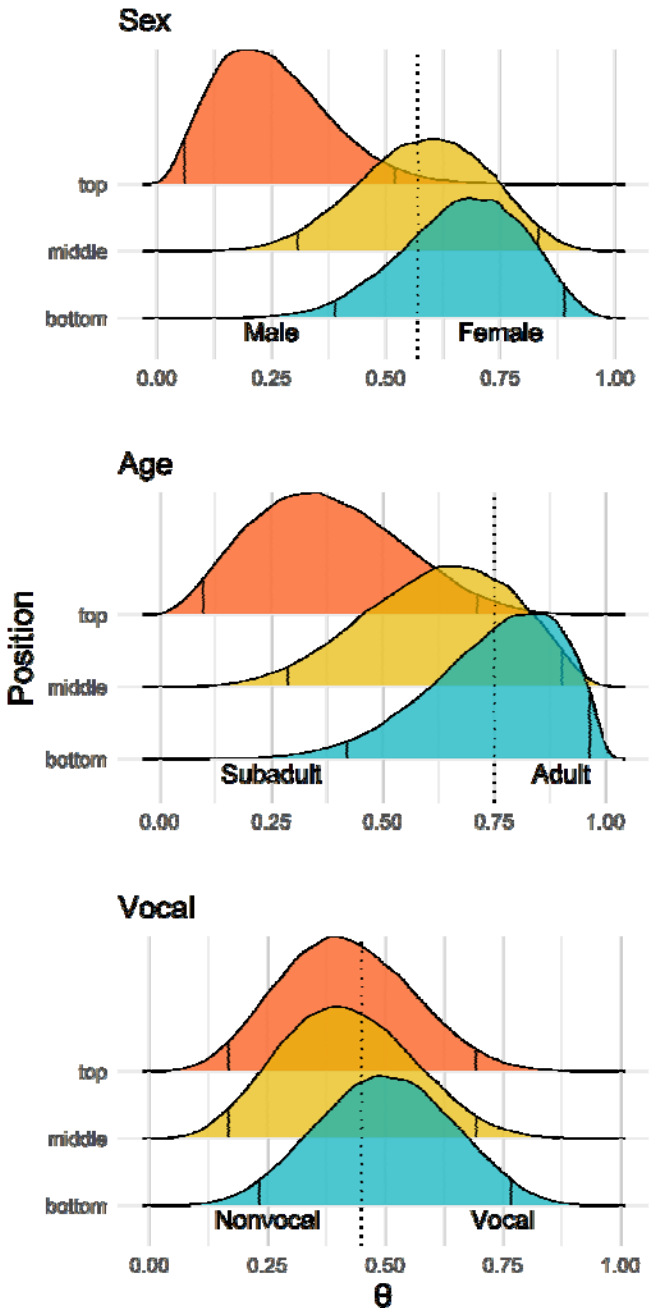

Figure 1. Distribution of posterior probabilities (θ) for the dominance index (David's score) according to sex, age, and vocal behavior. Dotted lines represent the values expected under the null hypothesis. Vertical lines within the curve indicate the 2.5% and 97.5% tails. Support for the alternative hypothesis, in either direction (male-female, adult-subadult, vocal-non-vocal), is shown whenever the majority of θ values (> 97.5%) fall above or below the dotted line.

DISCUSSION

In this study we investigated the consistency of individual positioning within the roost in a highly mobile and social bat species (*T. tricolor*). Our results provide the first evidence that bats can consistently position themselves in a predictable manner despite being forced to change roosts daily. We found greater consistency in peripheral positions (top and bottom), while central ones were more labile. Previous studies have also shown that communally-roosting species exhibit consistent positions within roosts, and that individuals often scramble to gain access to central positions which tend to be more labile than peripheral ones; the latter suggests some form of dominance hierarchy (McGowan et al., 2006). We also found that, when choosing the position inside the roost, there is segregation according to sex and age, which might hint at the presence of variation in resource holding potential or some mechanism that prompts familiar group members to scramble for positions in a predictable manner. Considering the evidence from our study in comparison to others', we suggest that dominance relationships could also influence how bats position themselves within roosts.

High scores for linearity measures within social groups of *T. tricolor* indicate that bats position themselves in a predictable way within the roost, suggesting that relative positioning may depend on 1) relative cost/benefit associated to each position and 2) dominance relationships within the social group. Considering the tubular shape and the verticality of the leaf, the top position might expose bats to the inclemency of the weather, particularly during the rainy season, and to direct attacks of predators that approach the roost from above. Alternatively, being on top may allow bats to escape predators approaching the roost from below. A bat in the bottom position would be protected from the rain but would leave the roost last in the event of a predator's attack, thus potentially increasing its risk of predation. Considering the pros and cons

of the top and bottom positions, we speculate that the middle position is the one that provides the greatest advantages. Central positions have consistently been shown to be more advantageous than peripheral ones (McGowan et al., 2006; Rayor & Uetz, 1990), and our study provides initial evidence that suggests a similar trend for bat groups roosting within developing tubular leaves.

Suppose there are differences in the costs and benefits of certain positions within a roost. In that case, individuals will most likely attempt to secure access to the one that provides the greatest benefits and fewer costs. These repeated interactions for access to a preferred position within a roost will likely result in dominance hierarchies. Typically, dominance hierarchies in mammals have been studied in the context of limited resources such as food (e.g. Wittig and Boesch 2003), yet our study suggests that similar interactions may occur in the fight for preferred positions within roosts, similar to some gregarious bird species (e.g. long-tailed tits, McGowan et al. 2006). Further studies are needed to understand which interactions occur within roosts as bats scramble to secure a preferred position.

In dominance hierarchies, differences in priority of access to resources is established through the resource holding potential (RHP; Parker 1974; Taylor and Elwood 2003). In this study, we found that males and subadults tend to occupy the top position more often than expected by chance. If in fact the middle, or central, position is the preferred one, given the lower consistency in the selection of that location, then our results could support our initial prediction that adults and females have greater RHP and thus relegate subadults and males to the potentially least preferred, riskier, position. Although we cannot unambiguously interpret our results as outcomes of dominance hierarchy relationships within the group, because we did not investigate antagonistic behaviors between individuals, this positioning pattern is likely to be associated with different social ranks. We also expected vocal bats to be positioned at the

bottom, given that previous studies demonstrate that these individuals are usually the ones to locate roost sites (Sagot et al., 2018). Interestingly, we did not observe a higher probability of vocal bats being at the bottom, suggesting that bats may switch positions once the entire group has entered the roost. The latter would unambiguously demonstrate that positions may not necessarily depend on the timing of arrival, but that individuals scramble to select their preferred position once inside.

In conclusion, our results demonstrate that bats of the species *T. tricolor* consistently position themselves inside the roost despite its extreme ephemerality and the high mobility of the species. Whatever the mechanism(s) for the consistent positioning within the roost, this predictable behavior suggests that different positions expose individuals to different costs and benefits. Further research is necessary to understand the latter, and whether dominance relationships represented by antagonistic behaviors influence individual positioning. Typically, the role of roost sites in bats is primarily regarded as promoting affiliative interactions, such as allogrooming, mating, sharing food, and nursing, among others (Kunz, 1982). Our results suggest that roost sites may also serve as venues for establishing relationships based on antagonistic interactions. We also provide initial clues of the formation of dominance hierarchies within social groups, which to date have been rarely identified in bats (Kerth, 2008; Wilkinson et al., 2019).

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DATA AVAILABILITY STATEMENT

Analyses reported in this article can be reproduced using the data and code provided in the Figshare repository (https://doi.org/10.6084/m9.figshare.19709485). Additional data may be found in Supplementary Materials.

AUTHOR CONTRIBUTIONS

Conceptualization: G.G, G.C.; Methodology: G.G, G.C.; Investigation: G.G., S.C.-R., H.A.H.-P., J.P.B.; Formal analysis: G.G, G.C.; Resources: G.C.; Data curation: G.G., G.C.; Writing - original draft: G.G., G.C.; Writing - review & editing: G.G., S.C.-R., H.A.H.-P., J.P.B., G.C.; Visualization: G.C., S.C.-R.; Supervision: G.C.

ETHICAL STATEMENT

All sampling protocols followed guidelines approved by the American Society of Mammalogists for capture, handling and care of mammals (Sikes et al., 2016) and the ASAB/ABS Guidelines for the use of animals in research. This study was conducted in accordance with the ethical standards for animal welfare of the Costa Rican Ministry of Environment and Energy, Sistema Nacional de Áreas de Conservación, permit no. SINAC-ACOPAC-RES-INV-008-2017 (Decree

No. 32553-MINAE). Protocols were also approved by the University of Costa Rica's Institutional Animal Care and Use Committee (CICUA-42-2018).

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