

Article ID #514

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

Authors: Giada Giacomini, Silvia Chaves-Ramírez, H. Andrés Hernández-Pinsón, José Pablo Barrantes, Gloriana Chaverri

Peer Community In Ecology
Dr. Corina Logan

Dear Dr. Logan:

Thank you for the opportunity improve and resubmit our article #514, and for the time taken for finding reviewers and handling the revisions of this work. We find the comments and feedback given by three referees to be very constructive and helpful in improving the quality of our manuscript. We have carefully addressed these comments and the feedback given by the reviewers and believe that this new version of our manuscript has improved significantly and conveys the key message in a clearer manner.

We submit the revised version of our manuscript for your consideration for recommendation. Please find our point-by-point responses below, as well as the revised manuscript.

Best wishes,
Gloriana Chaverri on behalf of all authors

POINT-BY-POINT RESPONSE LETTER

RECOMMENDER'S COMMENTS TO AUTHOR:

Line 219: suggest how to measure social dominance rank in future studies because using the word dominance here could be confusing with how you measured dominance in this study, which was not about social dominance rank, but rather physical position. See reviewer 1's suggestions for how to rename this term.

Authors: We have modified the sentence as follows: *“Considering the evidence from our study in comparison to others’ (McGowan et al., 2006; Rayor & Uetz, 1990; Summers et al., 1987), we suggest that future studies could identify if dominance relationships, those in which subordinate individuals submit to dominant ones in contest situations (Kaufmann, 1983), could also influence how bats position themselves within roosts.”*

Reviewer(s)' Comments to Author:

ANNEMARIE VAN DER MAREL (MAJOR COMMENTS):

I have one major comment. I'm afraid that the authors do place too much emphasis on dominance throughout the paper, while they do not directly measure it and actually state that at the end of the intro (line 89-91) and highlight that in the discussion (lines 249-252). I think that if the authors want to use dominance throughout the ms, they will also have to study whether the position in the roost are fought over by the bats. As the definition of dominance is the relationship between two individuals which can be explained that one individual (the subordinate) will submit to another (dominant) individual in contest situations (Kaufmann, 1983). The dominance measure (lines 146-153) is not really dominance in this sense, and I think the authors could get at the question whether individuals use specific positions using a different method (see below). So, I would place less emphasis on dominance, as the paper tests whether bats prefer certain locations within a roost, not whether these locations are contested over. The authors can then use the results presented here to only discuss the possibility of dominance in these bats.

Authors: We agree with the reviewer and have tried to reduce the emphasis placed on dominance throughout the paper.

Also, before performing the linearity analysis, I would first like to see the basic measure of the number or proportion of times each individual per social group is located at each position. Then the authors can randomise the locations 100 or 1000 times and compare the observed proportion to the expected. This method would allow the authors to see whether the individuals use the same locations repeatedly or whether roost positions are random. This method is more direct to getting at whether there are consistent individual positions within roosts as highlighted in the title then using dominance.

Authors: We have added a new supplementary figure 1, that includes the proportion of times each bat, per social group, is located at each position, in addition to the results of the suggested randomization.

As of now, I find the title a little misleading as the authors do not directly answer consistent locations within the roost. The authors can use the linearity measure to test whether there is a certain preferred direction of roost positions.

Authors: We believe that all our estimates, linearity, the new comparison of observed and expected proportion of times spent in each position, and David's score, show that bats' relative position within the roost is consistent. Therefore, we would like to keep the same title of our paper.

I would remove the David's score altogether. Perhaps what would work better is creating a matrix of the different positions and then including the number of times adult females are occupying each position. A different matrix is created for adult males and then a mantel matrix correlation test can analyse whether these positions differ between sexes. The same can be done with age classes and vocal bats. I'm not certain whether this is the right method here but to me, it seems to get at the questions more directly of consistent individual positions within a roost and who occupies those positions than the linearity and david's score measures.

Authors: While we appreciate the advice, we don't believe the suggested analysis is suitable to our data. For example, how do we account for the effect of group identity when comparing matrices? This is relevant since groups were not observed an equal number of times, and so the counts per cell in a matrix would be biased. Maybe the reviewer can let us know why the Linearity and David's scores are not suitable, and based on this we can search for other options. However, the selection of these measures was based on an intensive search of options and inquiries to other authors, for example Hal Whitehead (author of SOCPROG which we used for estimating these metrics). I am not saying there are no other better options, just that we don't know which ones, or why there would be a need to change what we have so far.

ANNEMARIE VAN DER MAREL (MINOR COMMENTS)

Line 37-40: This is too much of a speculation. Please consider ending the abstract with a significance statement of the results provided in the paper not a speculation of the factors potentially explaining the finding.

Authors: We have followed the recommendation and have ended the abstract with a significance statement rather than speculate on a topic that was not directly addressed in our study.

Line 53: what is meant by this? The spatial position or consequences of social living. Please provide a noun after this.

Authors: We have added "spatial positions" to clarify.

Line 62-63: I would also think that attack strategy has an influence. A bird of prey could also attack individuals in the middle of a group, while an ambush predator would have better luck on the periphery.

Authors: We have added this information, and relevant references, to the sentence.

Line 64-65: as this is a general intro sentence, the authors could decide to include other examples besides roosting in bats, such as ground-dwelling rodents that rest in burrows, birds in their nests, and hibernating animals. Please also include references.

Authors: We have added references that include other taxa, in this sentence and the next. We have also removed the reference to bats so early on, to make it a more general introduction as suggested.

Line 67: "Roosts have heterogeneous internal conditions," Please provide a citation.

Authors: Added 2 citations.

Line 69-70: This is a very sudden change in direction. Consider moving this sentence to after line 74 of the examples.

Authors: We have decided to leave this sentence here, as it is a prediction based on the initial statements in the paragraph, and the examples of taxa are supposed to provide evidence that stationary animal groups follow that prediction. I have modified the sentence to ease the transition between ideas; hopefully this is now better.

Line 71-74: Can you provide the ref for each specific example, so that the reader knows which one belongs to which study? Also, the authors can remove the filler words "it has been found that".

Authors: Modified as suggested.

Line 80: Are these bats nocturnal? This would also provide another reason to study location in roost sites as it is hard to observe social behavior of nocturnal animals.

Authors: We have added a couple of clarifications to this sentence. This species is nocturnal, yet we studied their daytime roosting habits.

Line 84-86: Do the bats use one specific plant or multiple different plants? Please also provide some specifics about the plant species. And just out of curiosity, the bats can use the leaves for max one night?! Is it difficult for the bats to find suitable roost sites or are these specific plants very common and provide ample opportunities for the bats to find a new roost site daily?

Authors: We have added information about the plants used, at least the most common ones. And yes, these species of plants are abundant in many sites (ca. 7 to 70 furled leaves daily per hectare).

Line 87-91: I like the explicit mention that the authors do not study the function of the different positions and that this study allows the development of novel hypotheses. See also my major comment.

Authors: Thank you for your comment. We agree in that the paper focuses strongly on dominance, and we have tried to decrease the overall emphasis on this topic throughout.

Line 99: As the authors do not study dominance directly, I would not use dominance here. Instead, just mention that females and adults will occupy certain positions more than expected.

Authors: We have modified the text.

Methods

Line 120: "...are considered to belong...'

Authors: Modified as suggested.

Line 124: how did the authors trap the bats?

Authors: We have explained how we trap bats.

Line 128-130: A little more info about the vocalization recording would be helpful and then refer to the ref if readers require more detail. Right now, I'm curious how long you would record for if the observers just noted it down or also recorded the vocalizations, whether you can identify which bat is calling within the roost site. I like to know these things without having to read another paper.

Authors: We have provided more details on how we performed acoustic trials.

Figure 1: Love the drawing!

Authors: Thank you!

Line 136: I would first like to see whether the bats consistently position themselves in the same spot without any 'dominance' measures. See major comment.

Authors: See responses to major comments.

Line 139: it's a little misleading as I would think that the first one to enter the roost would be positioned on the bottom, so I would say 'bat a is always in the bottom'. If I'm wrong, please clarify.

Authors: Although I think we are talking about the same idea, I can see what you mean, that it would make more sense to explain this in the order in which the bats would position themselves inside the leaf as they arrive (although the order in which they enter may not be the same as the order in which they stay the entire day within the leaf roost). Therefore, I have modified the text accordingly.

Results

Figures: the figure quality is not really great.

Authors: I think the online system decreases the resolution of images. I have created them using high resolution and will provide these if the paper is accepted.

Figure 2: Can the authors also include the observed data points? Perhaps using a raincloud plot instead. I would also change the x-axis legend as it is now not clear whether bottom means starting at the bottom, etc.

Authors: Great idea! We have added data points to the figure. We have kept the x-axis labels so that they are identical to the names used in figure 1.

Discussion

Line 216: Can you also restate which positions are preferred by sex and age class?

Authors: We have restated this as suggested.

Line 219: can you provide the refs for the 'other studies'?

Authors: We have added the relevant references.

Line 230-232: Could there also be a thermal advantage for being in the middle or does that not matter for bats in Costa Rica?

Authors: Maybe it does matter, but we prefer not to speculate on this topic without having more evidence. This is a topic we would like to explore in future studies!

Lines 234-242: This is quite speculative. I would not create a whole paragraph on a situation that may or may not be. Perhaps it's primarily the affiliative relationships that decide where each bat will be positioned. Instead, the authors can state something along the lines of 'further research is required, to study the costs and benefits of certain positions as this may further highlight the possibility of a resource holding potential and a dominance hierarchy in these bats.

Authors: We have deleted this paragraph to avoid speculation.

Line 243-244: I would not start this paragraph with this sentence. Instead, first state your results and then discuss the implications.

Authors: We have removed this sentence for clarity.

Line 252=258: consider making this its own paragraph.

Authors: Modified as suggested.

Line 265-266: this is the first time mentioning the function of roost sites. Consider moving this already to the intro when introducing roosting in bats and highlighting the function in a separate paragraph in the discussion, perhaps instead of the dominance paragraph (lines 234-242).

Authors: The function of roost sites was already mentioned in the introduction, second paragraph (*"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"*).

ANONYMOUS REVIEWER 1 (MAJOR COMMENTS)

1) I highly missed details in the description of the statistical analysis. Perhaps I am not familiar with the Bayesian test applied, but I think that more complete descriptions and an explicit definition of the models used will improve the possibility of other researchers to replicate analyses. For example, it is not clear to me how repeated measurements of different groups entered the model. I also do not think it is clear whether sex, age and vocal capacity were considered together at the same model or not.

Authors: We have added some information to clarify the analyses in the Statistical analysis section.

In line 168 it seems to indicate that only one individual per group was considered. But in line 154 it seems to indicate that linearity and dominance were computed per group only, and

not individual. However, if the latter I am not sure whether repeated measurements were included already in this point. So, I am not sure to be reading this well, but if only one individual per group was considered why not include all individuals in each group, controlling for variation within groups? Again, if more detail regarding analysis can be given it would be highly valuable to the manuscript.

Authors: We have added some additional information (see previous comment and response), so hopefully this will clarify things.

Furthermore, if the authors only used one value per individual and per group did the authors tested for the consistency/repeatability of the individuals' position across the different sampling periods?

Authors: In our original section "Linearity and dominance" we explain that David's score accounts for consistency in positions. *"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)."*

Finally, in line 171, does this refers to evaluation of the expected value under each null hypothesis? In that case, was the null hypothesis computed with the Bayesian binomial test and the expected values are according to the data (proportion of females = 0.57 in the collected data). Please clarify.

Authors: We have added some additional information (see previous comment and response), so hopefully this will clarify things.

2) I suggest clarifying the meaning of the measurements. In line 146 it is described how dominance was calculated, but then in line 250 it is assumed that the results do not indicate dominance hierarchy or dominance per se because it was not computed from aggressive interactions. I agree with this interpretation, which is reasonable, however I think the authors should state clearly from the beginning how this dominance measurement will be interpreted. Otherwise, the different parts of the manuscript may be a little contradictory.

Authors: We have tried to explain in greater detail the meaning of the measurements used in the second paragraph of the section "Linearity and dominance". We hope this clarifies things.

3) The authors present results for linearity measure (line 183: "linearity was greater and less variable when calculated from bottom to top positions"), however no statistical analysis seems to be described regarding this result. Did the authors assessed this only looking at Figure 1? If so, that should be explicitly stated. In any case, if no statistical test was performed, I think the authors can test whether the variance and values statistically differ among categories.

Authors: We have now added, in methods, the tests used to compare mean values and variances of linearity values. Here is the added text: *"To determine which position, bottom, middle or top, was associated to a more consistent placement of bats, we first compared*

variation in linearity values among positions using a Levene's test. The results of the Levene's test were significant ($F_{2,27} = 4.62$, $P = 0.01$), indicating differences in the variation of linearity values among positions. Given the latter, we used a Welch's ANOVA to test if there were differences in the values of linearity among positions, applying pairwise t-tests, with no assumption of equal variances, to compare linearity estimates among positions."

This is the new results section based on those analyses: *"The results of the Welch's ANOVA ($F_{2,14} = 3.74$, $P = 0.05$) suggest that linearity varies among positions. The pairwise t-tests show, however, that linearity did not differ significantly among positions (p -values: bottom-middle = 0.11, bottom-top = 0.19, middle-top = 0.33). The results of Levene's test ($F_{2,27} = 4.62$, $P = 0.01$) also show significant differences in the variation of linearity measures among groups within certain positions: the values of all groups for the bottom and top positions are consistently high, whereas there is greater variation in values for the middle position. The latter suggests that peripheral positions are more stable while central ones are mostly unstable."*

ANONYMOUS REVIEWER 1 (MINOR COMMENTS)

Line 59: please mention in which direction predation rates may be affected by their position.
Authors: We changed the sentence to "For stationary groups, studies have shown that individuals are often positioned predictably either on the periphery or the center of the group, and that the former are more vulnerable to predation (Rayor & Uetz 1990; McGowan et al. 2006)".

Line 100: I think the sentence would read better this way: "we predict that dominance over positions within the roost will be primarily assigned to adults and females, which are larger than males"

Authors: Thank you for the suggestion. We have modified the sentence as follows: "Therefore, in our study we predict that females, which are larger than males (Chaverri & Vonhof 2011), and adults will preferentially occupy certain positions within the roost".

Line 130: please briefly explain the method used to quantify vocal behaviour

Authors: We have added that information in the methods section (second paragraph in section "Data acquisition").

Line 140: was linearity computed per individual per scan or per individual across all scans? More details at which level was linearity (and other measurements) computed could help to clarify analyses.

Authors: Linearity produces one estimate per group per position. We added this information to the methods section.

Line 184: typo, Figure 2

Authors: We could not find the typo.

Line 191: does supplementary table presents the data? If so, it could be mentioned here.

Authors: The supplementary table was already mentioned in this section in the first version of the manuscript, as it does present the data on David's score.

Line 197: In the end of the sentence, I think it is missing a reference to Figure 3.

Authors: We have added a reference as requested.

Line 201: typo, Figure 3

Authors: We could not find the typo.

Line 212: this sentence mentions previous studies but does not mention the references to them. It could also be useful to include the taxa or species studied to understand whether this is reported to happen in a specific taxa or species only.

Authors: We have added an example (long-tailed tits) based on the reference provided.

Line 253: are these previous studies also in bats?

Authors: We have clarified that we are referring to the study species, *Thyroptera tricolor*.

ANONYMOUS REVIEWER 2

This an extremely well-written paper that explores an interesting aspect of relative spatial positioning, namely the positions occupied by different age-sex classes of individual Spix's disc-winged bats within a tubular leaf roost. Its findings are a relevant addition to this literature base, although only ten social groups were sampled; it is not clear how representative a sample this is, or how these groups were selected.

Authors: We thank the reviewer for the encouraging words! We now explain in greater detail our sampling and selection of groups in the first paragraph of the section "Data acquisition". See responses to specific comments below.

The introduction provides adequate context and justification for the study. The Methods could be improved by adding a little more information, as outlined below, to help the reader understand exactly how this study was conducted. The figures in the Results section are very clear and useful to the reader to understand the study's findings.

Authors: We have changed the methods as suggested (see previous comment and response).

Minor edits suggested would be to include a little more information regarding the leaf roosts in line 85 (do these only last for one 24 hour period? Why?).

Authors: We have added additional information to clarify: "*The latter occurs because the tubular shape of furled leaves of plants in the order Zingiberales (e.g., Heliconia, Calathea, Musa) used as roost-sites unfurl 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.*"

In line 124, please clarify what is meant by the "first encounter", and give more details about trap and release procedure; how much time was left between captures and data collection?

Authors: We have included additional information, as requested, in the first paragraph of the section "Data acquisition".

Could trapping affect individuals' behaviour in the short-term?

Authors: Yes, trapping would certainly change the position of individuals within the roost that same day. However, since bats change roosts every day, we expect bats will resume their normal behavior, at least as it pertains to positioning within roosts, the next day after being captured.

In the Methods section, please give further information on sampling effort – you give the dates of data collection, but the reader has no information on how frequently sampling was carried out.

Authors: We now provide additional information about sampling effort: *“We collected data on *T. tricolor* roosting behavior between November 2017 and May 2018 at Barú Biological Station in southwestern Costa Rica. We consistently searched the “Pizote” and “Vuelta del Zahíno” trails, an area of approximately 8 ha where we had previously found groups of bats, for a total of 41 days. Each day we searched for furled leaves to identify potential roosts, i.e., leaves which are occupied by a set of individuals (between 1-11, average = 5; Chaverri & Gillam, 2016); bats found in the same roost simultaneously are considered to belong to the same social group.”*

It would also be helpful to give information about this species' life history – was sampling carried out during the breeding season, for example?

Authors: We added the following sentence to the first paragraph of the “Data acquisition” section: *“During this period, most females are in the early stages of gestation; parturition first occurs in February (Chaverri & Vonhof, 2011).”*

In the Results section, you mention ten groups were sampled. Is there any information on population size so the reader can determine whether this was a representative sample?

Authors: Unfortunately, we don't have an estimate of group size. Despite that, we have added the following sentence to provide an idea of sampling effort: *“We collected data from all bats found within our sampling area, which comprise a total of 18 different social groups. For analyses we only considered groups that were observed on 5 or more days.”*

What about the population's range – what proportion of this was sampled?

Authors: The study species is found throughout the wet Pacific lowlands of Costa Rica. I would not risk speculating about what proportion of the entire population we have sampled.

Line 184 – figure name missing; line 201, incorrect figure number.

Authors: We have fixed these mistakes.

Line 226 – can you give the reader an idea of the types of predators bats are at risk from and perhaps their likelihood of attacking from either below or above, if this information is known?

Authors: We have added the following information to this sentence: *“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, such as monkeys and diurnal birds of prey (Boinski & Timm, 1985). Alternatively, being on top may allow bats to escape predators approaching the roost from below, such as snakes (Esbérard & Vrcibradic, 2007).”*