

In this study, the authors investigate the effects of social organization and social network connectedness on behavioral synchronization of individual animals. On free-ranging horses that show multi-level societies, they compare empirical data and model simulations to reveal interesting associations between social units, social interactions, and the propensities for animals to synchronize resting and movement states both within and across social units. The study provides novel insights into the movement ecology of multi-level societies, which remain largely understudied despite a recent wave of analytical work. Aside from its novelty, I found the manuscript to be well-written, with the authors also making informed decisions regarding their design and implementation of model simulations.

I nevertheless have a series of (mostly minor, but some major) concerns and comments I feel that the authors should address prior to deeming this work fit for publication:

Comments

Abstract

I feel that the summary is missing a final line of discussion, on the biological relevance of the authors' findings. Specifically, what does your finding that behavioral synchronization occurred at the intra- and inter-unit level mean for our understanding of horse social structure, or more generally of multi-level societies?

Introduction:

P2 L29: Provide a definition of "synchronization" here, before you emphasize why it is important (as you do in the rest of the paragraph). I come away from this paragraph knowing that it is important to study synchronization of behavior, but not necessarily what it actually means.

P2 L37: Here I feel that the authors could add a short paragraph, may be 2-3 lines, on what we know about the socioecological or biological importance of behavioral synchronization. For instance, is synchronization important to cohesion, social stability, resource finding or access, or predator avoidance? Is it linked to fitness and survival (other such advantages/benefits)? If there are any studies that, in addition to just examining evidence (or lack thereof) for behavioral synchronization, get at the above links, then review them here. Alternatively, review them within the follow-up paragraph in which you focus on reviewing the evidence for behavioral synchronization in single-layered groups/species.

P3 L71-75: These two sentences don't quite make sense, and need to be re-worded. Firstly, do you say "the behavioral synchronization", or just "behavioral synchronization"? The second sentence could be:

“Although the mechanisms underlying behavioural synchronization remain unclear, they are important to study and unravel in multi-level societies in order to better understand the collective features of such societies.”

Related to this sentence, are you actually trying to understand the mechanisms (causal factors) of synchronization here, or just whether or not there is within- versus between-unit synchronization in the first place? If, as I believe, it is the latter, then perhaps don't even use the word “mechanisms” here. I would just say something like:

“Whether multi-level societies show behavioural synchronization remains unclear, but it is important to address this question in order to better understand the collective features of such societies.”

P3 L79-80: Re-word for better clarity as:

“..., which showed a two layered structure of units (DEFINE) nested within a herd (DEFINE)”.

P3 L82-83: Again, I am left wondering as to what exactly you mean by “a model of behavioral synchronization”, or specifically “synchronize their behaviors” here. It would be good to re-state a definition for “behavioral synchronization” here.

Methods:

P4 L123: Could you better define how you identified and distinguished a ‘young individual’? Also provide more details regarding how you distinguished between males and females. Did you use any of the physical features that you list in line 114 for this?

P6 L191: Here I feel that a lay-reader would benefit from having an overall description of the model up front, rather than further down under *Model Design*. After you outline your overall goal, it would help to have 2-3 lines describing what type of model you used to achieve this goal, and what the model does to achieve the same. In other words, perhaps move the first 2-3 lines under the *Model Design* sub-section to up here, and also state following this line that you used (for example) *this general model design to test specific hypotheses pertaining to the effects of social organization on the synchronization of behaviors* (you don't have to state each individual hypothesis here, but give just the big picture). I feel that this would help the reader better follow the overall purpose of constructing these models.

P7 L205-207: Is this a fair, and a common, assumption to make, considering the large population sizes and the cohesivity (or lack thereof) of the social organizations that we are dealing with here? For instance, would this “awareness” not depend on the network connectedness of animals, i.e. differ in accordance with whether or not an animal was part of your own sub-group? Or on ecological visual barriers like trees, unless we are to assume that there were very few of these...? It may well be that I am missing something here, but could you

better justify or explain this assumption, perhaps also cite previous work that has also made this assumption?

P7 L215-218: From this, I gather that information regarding animals' changing states and social behavior were input in the model. By "social behavior", do you mean their social network connectedness? Given that you identified individuals' sex, would you also expect sex-based differences? If so, and more generally, is it possible to incorporate individual attributes (sex, age, but also social attributes like rank, node-level social connectedness or centrality, or size of the unit or community) in addition to, or instead of, dyadic attributes in your models? More generally, would asking whether *individuals* of certain attributes sociodemographic characteristics and attributes have a greater-than-expected tendency to synchronize their behaviors be an interesting question to ask in the first place?

If this is difficult to pull off given the scope of these models, then perhaps the authors could at least speculate (in the Discussion) on how individual and attributes and characteristics might influence their propensities (or lack thereof) to synchronize their behaviors.

P7 L222, 225: Supplementary (material?)

P8 L234-237: This line doesn't seem to make sense. Consider re-wording for better clarity. Did you mean to say "*irrespective of the individual*"?

P10 L308: I reckon this should be "model fit", not "fitness of models".

P10 L311: Change to "each 30-minute window".

P11 L315: Could you better justify why you used a non-parametric (K-S) test here? I guess it was it because of the inter-dependencies of dyadic data, but isn't that why you used Mantel tests? More generally, why use both K-S tests and Mantel tests? Perhaps I am missing something here...

P11 L327-329: Could you better explain what 'score' was used to determine the extent of deviance from the null? I am guessing that this 'score' is simply, as you state in the previous line, the proportion of models that showed better results, than the null, in terms of being able to predict the observed data. If this is correct, please explain this better in the last line, otherwise provide more details here on how you calculated this 'score'.

Results:

P11 L346: This first line is probably not necessary, since we know by know as to what these models function for.

Discussion:

P12 L370: I would also be clear and say “synchronization of behaviors” here. So perhaps say “...dynamics of behavioural states, specifically the synchronization of resting versus movement,...”

P13 L417: See my comment regarding P7 L215-218, and thoughts on how the authors might provide a short paragraph here speculating on how inter-individual differences in attributes (e.g. age, sex, rank, centrality) might affect behavioral synchronization.

P14 L418: See my comment regarding your assumption on P7 L205-207. I understand that the simplicity of your model would make it broadly applicable. That said, could you say something here about whether the (key) assumption you made regarding animals’ awareness of the states of other animals at any given time is *also* broadly applicable? For instance, how would that differ across, say, horses that presumably live in open plains, and nonhuman primates living in multilevel societies that inhabit tropical and temperate forests where the vegetation is more dense?