Review of: "Reproductive skew, fitness costs, and winner-loser effects in social-dominance evolution"

Lucy Oldham

Potential competing interests: The author declared that no potential competing interests exist.

Overall, I find this to be a good quality and enjoyable article to read. The model allows new hypotheses to be tested, such as the effects of availability of uncontested resources and of dominant monopolisation of reproduction on learning (winner-loser effects). However, the justification for this study in the introduction is weak and I had to re-read several sections to know what the independent and dependent variables were. I do not have experience of generating behavioural models, so cannot comment on the validity of your results, however having related interests in applied animal behaviour, I would have appreciated more clear presentation of results. To encourage collaboration, I suggest revising the abstract and introduction in order to clearly outline the need for such a model, and to ease the understanding of your results by readers from adjacent fields, to avoid overuse of acronyms and to explain your key terms more explicitly throughout. Please find comments on individual lines below:

Abstract

You describe your main findings well, but here the justification and application of the study could be briefly outlined in order to engage a wider audience.

The second sentence does not make it clear what you are really testing. You don't test the link between access to resources and reproductive skew, as I understood it, what you really test is the effect of different types of dominance structure and the cost of fighting, and the effects of dominance structure on winner-loser effects.

"Substantial costs of interacting"- not clear what you mean here, do you mean "death from fighting"? Final sentence: "We compare our results...", and what did you find? Why is it important/interesting?

Introduction

In general, this would be strengthened by making more definite statements about your aims. What is not known? You make suggestions on how the model could possibly be applied (e.g. line 32-34), but quite tentatively, which makes it harder to see why the study was needed. You ask some interesting questions about learning without really explaining what might influence the strengths of winner and loser effects. It could be useful to reference studies on assessment styles, and in this regard, to be explicit about what your assumptions are (e.g., all animals learn to use mutual assessment).

4-7, is this a key motivation for your study? If so, include in abstract. If not, suggest moving to line 30.11-13, best to provide citations to either give examples of where the costs of dominance interactions (i.e., fighting) have been studied, or systematic reviews which point to the absence of such studies.

20-21, What do you mean "genetically determined traits that function as parameters for the learning mechanism"? Do you mean RHP? Cognitive ability?

24-26: This could go in the methods section, unless you want to explain how your model builds on previous studies, in which case give an example.

34-36: This is quite a big limitation, is it realistic? Can you explain why you made all individuals unrelated?72: Helpful to briefly describe the previous model and what you have added.

94: Is this realistic? If both animals submit why are there successive rounds? Are there real examples where animals would keep fighting a contest after both have submitted?

103-104: Here you state the most important part of the study. I suggest explaining this earlier.

115: Make sure to pick this up in the discussion, as starting again from scratch assumes no individual recognition.

120: In your introduction you state this model could apply to both males and females. If they can have mating success without surviving the reproductive season, does this still hold for females? Evolutionary simulations

In this explanation, it would be much easier to follow if you used recognisable terms such as Aggression (instead of action A) and explain what you mean by "value" in the text (i.e. fighting ability).

142-143: Useful to repeat what these 8 individuals of the other sex represent in both cases (males and females). Are they of equal value?

Results

You have some really interesting results, I suggest summarising the key findings at the start, and maybe splitting this section up in a more logical manner by individual hypothesis.

172: Figure S1 is difficult to follow and to really know what the treatments are and what the labels represent.

182-185: V11-V14 are important variables, so explain in the text, and possibly in the figure labels, clearly what they mean.

188-193: This is well explained, but it could be in the methods section to help set up the study.

203-204: Using words to describe " f_i " would help understanding

209: I'm struggling to understand the logic, how can equally matched opponents not have a 50% likelihood of winning? Is it because of draws?

Figure 1: Panels A and B could be separated from C and D, or just explained clearly in the text. In 1 (b), the acronyms "AA, AS and SS" require reference to a separate table so the figure can't be understood independently. Suggest using words.

Discussion

Well written and interesting general discussion of your results. The later sections on application of the model are quite vague. To encourage collaboration and interest I think you need to more explicitly state what questions can be addressed by bridging the gap between models and empirical studies, and what information is needed in order to overcome some of the limitations of the model.

282: "Fairly much studied", reconsider word choice, this doesn't really say anything

283: "Of these"- clarification needed, of what?

297: This is the first time you've mentioned "common interest". To be more positive and highlight what your model was able to test (e.g. influence of uncontested resources), I would only introduce this limitation of the model later on.

252-254: Instead of introducing new information that isn't in the results, could this go in the methods as an assumption or justification for how you constructed the model?

256-257: Hard to follow this sentence, suggest rewording this and the previous sentence for simplification.

264-266: Important and interesting point, maybe emphasise earlier.

271-273: And also cost?

275: Figure 4 doesn't clearly relate to this sentence, or if it does, I did not understand this from the labels.

334-341: Why did you base your model on an unrealistic assumption then?

384: Suggest giving examples of more recent experimental papers.

405-407: Could you be more positive here? What are the challenges and solutions?

410-411: Important to note that personalities are *consistent inter-individual differences*, not just consistent behaviour over time. For example, ontogeny might mean that all animals become less aggressive over life, but the most aggressive individuals remain relatively so.

Modelling social dominance and aggression

This section drifts quite a lot from discussion your results and becomes too essay-like. Suggest picking the key points from the first 3 paragraphs and explain how your findings might be different if you used a purely small-world or large-world model.

466-468: Do you have any views on what are the priorities? This is quite vague and would be strengthened if you highlight the most important opportunities and unanswered questions.

Supplementary information

One of your assumptions is that the perceived reward of submission is zero. Work by Dijkstra*et al.* 2012,^[1] challenges this presumption. Might animals perceive a draw as rewarding if both opponents submit?

References

 Peter D. Dijkstra, Sara M. Schaafsma, Hans A. Hofmann, Ton G.G. Groothuis. (2012). <u>'Winner effect'</u> without winning: Unresolved social conflicts increase the probability of winning a subsequent contest in <u>a cichlid fish.</u> Physiology & Behavior, vol. 105 (2), 489-492. doi:10.1016/j.physbeh.2011.08.029.