Peer Community In Zoology

The unreliable signal: No correlation between forceps length and male quality in European earwigs

Olivier Roux *based on peer reviews by* ***Luna Grey*** *and 2 anonymous reviewers*

Samantha E.M. Blackwell, Laura Pasquier, Simon Dupont, Séverine Devers, Charlotte Lécureuil, *Joël Meunier (2024) Relationship between weapon size and six key behavioural and physiological traits in males of the European earwig. bioRxiv, ver. 3, peer-reviewed and recommended by Peer Community in Zoology.
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In animals, male weapons such as antlers, horns, spurs, fangs, and tusks typically provide advantages in male contests and increase access to females, thereby enhancing reproductive success. However, such large and extravagant morphological structures are expected to come at a cost, potentially imposing trade-offs with life history traits, physiological functions, or certain behaviors (Emlen, 2001; Emlen, 2008). These costs should be manageable only by males in the best condition. The present study by Blackwell et al. (2024) examines this assumption through a comprehensive study on the European earwig, where males possess forceps-like cerci that vary widely in size within populations.

In the European earwig (*Forficula auricularia*), male forceps are used in male-male contests as weapons to deter competitors prior to mating (Styrsky & Rhein, 1999) or to interrupt mating pairs by non-copulating males (Forslund, 2000; Walker & Fell, 2001). Despite providing benefits in terms of mating success (Eberhard & Gutierrez, 1991; Tomkins & Brown, 2004), it remains unknown whether long or short forceps are associated with other important life-history traits.

In this laboratory study, Blackwell et al. (2024) investigated two European earwig populations, each divided into two subpopulations: one with the shortest forceps and one with the longest forceps. They examined the potential costs of long forceps on six different traits: one reproductive trait (sperm storage); three non-reproductive behavioral traits such as locomotor performance (involved in search for resources), fleeing reaction face to a risk (long forceps are supposed to be correlated with boldness), and aggregation behavior (European

earwigs are facultative group-living organisms); and survival (when deprived of food and subsequently when exposed to an entomopathogenic fungus).

As males in the best condition are supposed to be those that can afford to develop large forceps, Blackwell et al. (2024) predicted that males with long forceps would perform better than those with short forceps across the investigated traits. However, their predictions were not validated, as no correlation between weapon size and male quality was detected in either population. Although the sample size is sometimes limited, the consistency of these results across different populations adds robustness to their conclusions.

By demonstrating that forceps length in the European earwig does not reliably indicate male quality, this paper challenges existing theories and highlights the complexity of evolutionary processes shaping morphological traits. Furthermore, the study raises important questions about the evolutionary mechanisms maintaining weapon size diversity, providing a fresh perspective that could stimulate further research and debate in the field, notably the search for other traits where costs might be incurred.

References:

Blackwell, S.E.M., Pasquier, L., Dupont, S., Devers, S., Lécureuil, C. & Meunier, J. (2024). Relationship between weapon size and six key behavioural and physiological traits in males of the European earwig. bioRxiv, ver. 3 peer-reviewed and recommended by Peer Community in Zoology. https://doi.org/10.1101/2024.03.20.585871

Eberhard, W.G., & Gutierrez, E.E. (1991). Male dimorphisms in beetles and earwigs and the question of developmental constraints. Evolution, 45(1), 18–28. https://doi.org/10.2307/2409478

Emlen, D.J. (2001). Costs and the diversification of exaggerated animal structures. Science, 291(5508), 1534–1536. https://doi.org/10.1126/science.1056607

Emlen, D.J. (2008). The evolution of animal weapons. Annual Review of Ecology, Evolution, and Systematics, 39(1), 387–413. https://doi.org/10.1146/annurev.ecolsys.39.110707.173502

Forslund, P. (2000). Male-male competition and large size mating advantage in European earwigs, *Forficula auricularia*. Animal Behaviour, 59(4), 753–762. https://doi.org/10.1006/anbe.1999.1359

Styrsky, J.D., & Rhein, S.V. (1999). Forceps size does not determine fighting success in European earwigs. Journal of Insect Behavior, 12(4), 475–482. https://doi.org/10.1023/A:1020962606724

Tomkins, J.L., & Brown, G.S. (2004). Population density drives the local evolution of a threshold dimorphism. Nature, 431, 1099–1103. https://doi.org/10.1038/nature02936.1.

Walker, K.A., & Fell, R.D. (2001). Courtship roles of male and female European earwigs, *Forficula auricularia* L. (Dermaptera: Forficulidae), and sexual use of forceps. Journal of Insect Behavior, 14(1), 1–17. https://doi.org/10.1023/A:1007843227591

Reviews

Evaluation round #2

DOI or URL of the preprint: https://doi.org/10.1101/2024.03.20.585871
Version of the preprint: 2

Authors' reply, 06 June 2024

Dear Olivier Roux,

Thank you for your detailed review of our manuscript and sorry for our persistent errors. We have made the latest corrections you suggested. In particular:

- We have provided a brief interpretation of the power analysis on your results: "The statistical power of each analysis ranges from 0.155 (sperm count) to 0.447 (survival in harsh environments; Table 1). These values suggest that the likelihood of detecting statistically significant effects based on the values reported in this study was sometimes relatively low, particularly given the large variance obtained for certain traits. Larger sample sizes, particularly for sperm count, may therefore be needed to confirm the absence of effects more robustly." (L

- We have changed "to two these" to "to these two"

- The references (Otte & Stayman, 1979; Emlen & Nijhout, 2000) have been added to the reference list.

- We have edited the legend of figure 2 to indicate that orange is the shortest and blue is the longest forceps

- We have edited Figure 3 to show short forceps (orange) on the left and long forceps (blue) on the right, as in Figure 2. Note that in doing so, we realised that there had been some confusion between the two populations in the figure (and in the main text). We have therefore edited the results and discussion accordingly. This does not change the interpretation of our results. We have also removed the reference to the shape of each population in the legend of Figure 3, as this did not apply to all panels of the figure and the populations are clearly written in all panels.

Sincerely,

Joël Meunier, on behalf of all co-authors

Decision by Olivier Roux, posted 05 June 2024, validated 05 June 2024

last minor revisions before recommandation

Dear Joël Meunier and co-authors

I have reviewed the revised manuscript and am satisfied that you have addressed the comments raised by the reviewers. There are only a few minor changes I would suggest before the manuscript can be fully recommended.

- Please provide a short interpretation of the power analysis on your results.

- Line 235: "to two these" should be "to these two"

- Line 275: "(Otte & Stayman, 1979; Emlen & Nijhout, 2000)". These references are missing from the final reference list. Please, check the manuscript.

-In the legend of the figure 2: orange one are the shortest and blue one are the longest forceps (not the opposite)

- Line 609, Figure 3:"Males came from Cinais (square) or Valence (triangle)", it is the opposite on the figure.

-Figure 3: this a detail but it could be nice to have, for each population, short forceps (orange) on the left and long forceps (blue) on the right, as in figure 2.

With kind regards,

Olivier Roux

Evaluation round #1

DOI or URL of the preprint: https://doi.org/10.1101/2024.03.20.585871

Version of the preprint: 1

Authors' reply, 04 June 2024

Dear Olivier Roux,

Thank you for your decision on the manuscript entitled "Relationship between weapon size and six key behavioural and physiological traits in males of the European earwig" we submitted for recommendation in PCI Zoology.

We have addressed all the reviewers' comments. In particular, we have added information to better detail why we measured each of the six traits, we have added a figure to clarify the timeline of the experiment and the associated variation in sample size, and we have added power analyses to confirm the robustness of our approach. We have also edited the text to take account of all the minor suggestions and corrections made by the reviewers.

Overall, we believe that these changes have significantly improved the clarity, robustness and impact of our study. We are therefore very grateful to the three reviewers for their constructive comments and suggestions.

We have also updated the link to the repository of our R script and dataset as we have included the new power analysis in the script.

A detailed point-by-point response to the referees' comments is provided in the attached document, together with a tracked changed version of the new manuscript.

Sincerely,

Joël Meunier, on behalf of all co-authors

Download author's reply

Download tracked changes file

Decision by Olivier Roux, posted 22 May 2024, validated 22 May 2024

Revision required

Dear authors

Your manuscript has been reviewed and reviewers are enthusiastic about the topic. However, they raised concerns about the methodology and the interpretation of the results. The choice of traits measured also needs to be justified so that the reader can better understand their relevance to this study. The weaknesses of the study should also be better highlighted.

Looking forward to your revision.

Kind regards

Olivier Roux

Reviewed by anonymous reviewer 2, 29 April 2024

In this manuscript, authors measured six behavioural and physiological traits in the European earwig under the hypothesis that having long forceps comes with some behavioural and/or physiological cost and/or strengthe for males. However, authors could not find any associations at least in six behavioural and physiological traits. According to the result, authors questioned that long forceps functions as "high quality signal". All of experiments are well described and their limitations are also clearly mentioned. I think this manuscript can be published in the journal.

In discussion section, authors carefully interpreted their results and significance with enough previous studies. Also, authors clearly stated limitations of their study and explained alternative possibilities. My only concern is that authors did not mentioned about ecological cost (such as predation rate and flight ability) of forceps. I think it is better to add possible ecological cost and/or benefic of forceps in discussion section.

Reviewed by anonymous reviewer 1, 21 May 2024

This paper explore the relationships between the size of extravagant forceps in male earwigs and several behavioural/physiological traits supposed to be linked with fitness (namely: locomotor performance, boldness, aggregation behaviour, survival under harsh conditions, sperm quantity and survival to pathogen exposure). The rationale for this study is that forceps length can be an indicator of male quality, but also that the forceps length can trade-off with other fitness-linked traits.

I found the study interesting in its aims, but I have several questions/comments about the experimental process.

1- The choice of measuring certain traits should be better justified in relation to their importance on animal fitness. For example, In what locomotor activity is important for earwigs? Is sperm count important? (the long duration of copulation mentioned to justify this measurement can also be due to mate guarding, therefore having no relationships with sperm count)…

2- L. 121-123: Prior to experiments, animals were maintained in groups for 3 months, so that it is highly probable that the males used were not virgin… What is the impact on sperm count ? (how to control that all males copulated or not before measurements?)

3- During the whole experiment, males were isolated and not fed. I would like the authors discussing this harsh condition. First, why is it so? Why not feeding them? Second Is there not a risk that the weakening of the animals will level down all their behavioral performances or sperm count, thus erasing all potential variation?

4- Two trait were measures after one-month isolation, during which only 15 to 50% males died, variable among groups and populations. There is therefore a risk for a differential selection of best individuals. Such a selection may confound sperm count and survival to pathogen infections.

5- The sample size gets smaller and smaller as time goes by. I suggest running a power analysis. I guess that owing the variation observed, sample size is too small to conclude firmly. At least there is no strong effect.

6- In Table 1, numbers in the last line are not consistent with those provided in the text (Where 39 individuals are given for sperm count and 52 for survival to pathogens).

7- L. 239. Aggregation score is at 0.05, so this result should be considered and discussed.

8- L. 252-253. There is a significant interaction between survival and population (Table 2). Therefore there is no “no effect”. Please be consistent with your own analysis.

To conclude, in the discussion, before discussing the background, I would like the authors acknowledging the potential weaknesses of their study that could confound the results (points 2-5 before). While discussing the limitations of most previous experiments is fine, it would be fair to discuss the limitations of the present one.

Does the title clearly reflect the content of the article? [X] Yes

Does the abstract present the main findings of the study? [X] Yes

Are the research questions/hypotheses/predictions clearly presented? [X] Yes

Does the introduction build on relevant research in the field? [X] Yes

Are the methods and analyses sufficiently detailed to allow replication by other researchers? [X] Yes

Are the methods and statistical analyses appropriate and well described? [X] Yes and [X] No (well described, but not always appropriate, see text)

In the case of negative results, is there a statistical power analysis (or an adequate Bayesian analysis or equivalence testing)? [X] No

Are the results described and interpreted correctly? [X] No (not always, see text)

Have the authors appropriately emphasized the strengths and limitations of their study/theory/methods/argument? [X] No

Are the conclusions adequately supported by the results (without overstating the implications of the findings)? [X] No (see text)

Reviewed by Luna Grey, 09 May 2024

· Title and abstract
o Does the title clearly reflect the content of the article? [X] Yes, [ ] No (please explain), [ ] I don't know
o Does the abstract present the main findings of the study? [X] Yes, [ ] No (please explain), [ ] I don't know
· Introduction
o Are the research questions/hypotheses/predictions clearly presented? [X] Yes, [] No (please explain), [ ] I don't know
o Does the introduction build on relevant research in the field? [X] Yes, [ ] No (please explain), [ ] I don't know
· Materials and methods
o Are the methods and analyses sufficiently detailed to allow replication by other researchers? [X] Yes, [ ] No (please explain), [ ] I don't know
o Are the methods and statistical analyses appropriate and well described? [X] Yes, [ ] No (please explain), [ ] I don't know
· Results
o In the case of negative results, is there a statistical power analysis (or an adequate Bayesian analysis or equivalence testing)? [ ] Yes, [ ] No (please explain), [X] I don't know
o Are the results described and interpreted correctly? [X] Yes, [ ] No (please explain), [ ] I don't know
· Discussion
o Have the authors appropriately emphasized the strengths and limitations of their study/theory/methods/argument? [X] Yes, [ ] No (please explain), [ ] I don't know
o Are the conclusions adequately supported by the results (without overstating the implications of the findings)? [X] Yes, [ ] No (please explain), [ ] I don't know

In regards to "Relationship between weapon size and sex key behavioural and physiological traits in males of the European earwig", I think that this paper presents an interesting set up to assess whether forceps length is actually a reliable signal for male quality. However, I feel that the methods could be clearer as to the timeline of the tests. Ideally, each of these tests would have been done prior to them being starved. Additionally, I would like a bit of clarification on why some of these traits were chosen. Some of the traits make sense (boldness, resilience to pathogens, etc.) but some I don't quite see the rationale for (e.g. aggregation). This is not to say there is none, but it should be stated explicitly in the text.

Comments

Line 23 – the sample size is a bit misleading here as I assumed that out of hundreds of individuals you chose these 120 individuals. I think this can be made clearer by saying something to the effect of: "selecting 60 individuals with the longest and shortest forceps from two populations and the…."

Line 24 – It would be interesting to explain why you chose these traits

Line 37 – This sentence is a little awkward, I would put the examples of extravagant structures in parentheses. "take a variety of forms (such as: antlers, horns, spurs, fangs and tusks), and work to enhance the male's fighting ability and/or attractiveness to females (Emlen, 2008).

General – first reference to a species should include the authority of the species.

Line 50 – the plural of prey is prey

Line 67 – Do you know if male earwigs have hyperallometric growth to their forceps? I think adding this information may help give context or explain the trends you are seeing, particularly about using forceps length as a proxy for male quality.

Line 78 – "or to interrupt mating by non-copulating males" is a bit confusing. May I suggest "or to interrupt mating individuals by non-copulating males". Originally it sounds as though the earwigs are interrupting their own copulation.

Line 81 – I would change "females do not seem to select their mate on the basis of forceps length" to "females do not seem to select their mate exclusively on the basis of forceps length" as I am sure that forceps length does play some role in female choice, even if a very small one.

Line 102 - I think these are all good traits to test individually. But I would like some rationale as to why you chose these traits in particular.

Line 160 – The setup for this section was a bit confusing. I think that having a diagram might help make this clearer.

Line 169 – I think this line can be simplified by rewriting it as: "We recorded whether …"

Line 176 – I think this should be moved up, perhaps at the beginning of the "Behavioural measurements" section (Line 144). There you can explain the timeline of your assessments and at the beginning of each test you monitored how many individuals were still alive and that you used this as an assessment of survival in harsh conditions.

Methods – While reading I was having a bit of a hard time understanding the timeline of when you did your tests and I think having a section detailing this would improve that understanding. This could be the first paragraph where you explain the behavioural measurements. Here you could outline when you were doing each test, when you were starving the earwigs and when the last test was conducted.

Line 186 – I think you mean "dissecting microscope"?

Line 195 – "mal" should be "male"

Line 198 - I think this should be its own section as otherwise the change in subject is too abrupt.

Line 234 – The "(not short)" in "long (not short) forceps" doesn't seem to clarify the point you want to make as clearly as possible. I think adding explicitly that this trend was not found with in males with short forceps is important.

Line 269 - I believe that this paper will help make this argument as this shows that there are alternate morph for this species, albeit very difficult to identify. "Tomkins, J. L., Kotiaho, J. S., & LeBas, N. R. (2005). Matters of Scale: Positive Allometry and the Evolution of Male Dimorphisms. The American Naturalist, 165(3), 389–402. https://doi.org/10.1086/427732"

Line 298 – I agree with all the possible reasons for this, but I would like to add that environmental conditions may be an important factor as well. Valence is a closed and forested area, the males from this region may be naïve to this type of perturbation.

Line 317 – I think "growing longer forceps" might be more concise.