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The measure of spatial position within groups that best predicts predation risk depends on group movement

Poppy J. Lambert, James E. Herbert-Read and Christos C. Ioannou

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Original submission: 9 June 2021
Revised submission: 30 July 2021
Final acceptance: 23 August 2021

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

Review History

RSPB-2021-1286.R0 (Original submission)

Review form: Reviewer 1

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
this is an interesting and well-written manuscript on measures of spatial position of prey depredated by sticklebacks and predation risk. Virtual prey was used in order to manipulate prey and calculate various spatial positions. Movement influenced which measure best predicted predation risk. I have only some minor comments for improvement.

Minor comments:
line 71: mention with what sticklebacks were fed. Did they have experience with foraging on Daphnia, which were obviously simulated as prey. Nowhere the reader is informed about the nature of the virtual prey. Please justify the choice of the virtual prey size and movement. To me the movement of the group looks artificial, that is unidirectional with a constantly slow speed. Nevertheless, you generalize the results in terms of movement but the results may strongly depend on the nature of the movement (like speed, direction, variability). Please discuss.

Give details of the illumination: how bright was the lightning. This may influence foraging. In the videos of the supplement, the virtual prey is seen on the front but also on the back wall. This is not the case in Fig. 1. Did the reflections on the back wall, if visible at all, influence foraging behaviour?

It would be very helpful to the readers if you could visualize the measures listed in Table 1 in a Figure.

Review form: Reviewer 2 (Ben Hirsch)

Recommendation
Major revision is needed (please make suggestions in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Excellent

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
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Is it accessible?
Yes

Is it clear?
N/A

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
The authors tested which methods for measuring an individual's within-group spatial position provided the most predictive power of predation risk in a simulated predation experiment. This is an extremely interesting paper on a topic very near-and-dear to my research interests. Interestingly, the authors found differences in which method works best depending on whether the group was stationary or moving. When groups were stationary, the limited domain of danger was the best predictor (over a broad range of pixel sizes), and when moving, the AoV was the best method (except for N near neighbors over a limited range of pixel sizes). More broadly, individuals in stationary groups were more vulnerable when local prey density was low, while individuals in moving groups were more vulnerable when close to the "group edge." This paper is well written, the statistic are appropriate, and overall, I really liked this paper. I also hope this paper brings more attention to the importance of how predation risk is measured. Despite a couple of (IMHO) very good papers (Stankowich 2009, Hirsch and Morrell 2011) discussing which measures should be used in different scenarios, I continue to see authors use inappropriate or sub-optimal methods of quantifying spatial position. In addition, the citation rates on these two papers are far lower than I think they should be. I hope that this paper will help change this. I do think that this paper could be revised/rewritten to more accurately reflect the results, and to put the results into better perspective. The experimental set-up isn't necessarily one I would have used, and I think a different set-up may lead to very different results. I highly suggest that the authors provide additional information/analyses to support their conclusions (details below). This experiment is similar to previous lab experiments of predation on simulated prey (Ioannou et al. 2019). The issue with this experimental setup is that the fish are attacking a 2D group of animals from "above." In general, 2D animal groups are on a landscape, and predators either attack them from the same plane (i.e. the old-school lion attacking a cow example), or above (i.e. aerial bird of prey attacking a flock of birds foraging on the ground). The choice of experimental setup should be a really important driver of the results. In the case of terrestrial predators attacking terrestrial prey, and the assumption that predators attack the closest prey (or at a

minimum, do not pass by close prey to get to another individual further away), a measure of spatial position relative to the group edge should be the most important determinant of risk. This is the rationale behind the Angle of Vulnerability (AoV) method tested here. In the latter case (aerial predation on terrestrial group), measures of local density could be predicted to be more important (although see Romey et al. 2008). It's also important to note that you are testing the predation behavior of a predator that normally preys on 3D groups (I believe?) with a 2D prey group. What affect does this change in dimensionality have on the predatory behavior of the fish? An interesting observation about this ms is that there are no a priori predictions about if these measures should differ between moving and non-moving groups, and if the authors predict that differences should occur, then which methods should work better in each condition. Following from my points above, I would assume that measures of local density would be better measures of predation risk in this scenario. This may change if the predator is approaching the "group" from one direction (because of the prey group movement). In the case when the fish have to swim over to the prey dots, they could be predicted to prefer targeting close individuals, in which case a measure of "edge" would be the better measure. If stationary groups were mostly targeted by fish attacking directly perpendicular to the prey dots, and if the moving groups were mostly targeted by fish attacking from "outside" the group, the results in this paper make perfect sense. I believe the authors can test this. What percentage of "attacks" were carried out by fish attacking from "above" vs "outside" the group in each treatment? If the patterns resemble my predictions here, I think the results are quite logical and easy to predict a priori. I would like to see the authors report these numbers, and write/revise the manuscript to reflect the experimental set-up more accurately,

Specific comments:
Line 46. And food acquisition! Very important, but not cited. Hirsch 2007 reviews some of the lit on this topic.
Lines 128-138. Why was this speed chosen? This seems really slow, but it's hard for me to really picture it in my head. Could the authors provide sample videos with the fish in the video? Could this slow speed be the reason why this study found no evidence of higher predation on front edge individuals when compared with Ioannou et al. 2019?
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Decision letter (RSPB-2021-1286.R0)

08-Jul-2021

Dear Ms Lambert:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers' comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your

reference. As you will see, the reviewers and the Editors have raised some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Associate Editor, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

To submit your revision please log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions", click on "Create a Revision". Your manuscript number has been appended to denote a revision.

When submitting your revision please upload a file under "Response to Referees" - in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Your main manuscript should be submitted as a text file (doc, txt, rtf or tex), not a PDF. Your figures should be submitted as separate files and not included within the main manuscript file.

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If your study contains research on humans please ensure that you detail in the methods section whether you obtained ethical approval from your local research ethics committee and gained informed consent to participate from each of the participants.

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If your study uses animals please include details in the methods section of any approval and licences given to carry out the study and include full details of how animal welfare standards were ensured. Field studies should be conducted in accordance with local legislation; please include details of the appropriate permission and licences that you obtained to carry out the field work.

Data accessibility and data citation:
It is a condition of publication that you make available the data and research materials supporting the results in the article. Please see our Data Sharing Policies (https://royalsociety.org/journals/authors/author-guidelines/#data). Datasets should be deposited in an appropriate publicly available repository and details of the associated accession number, link or DOI to the datasets must be included in the Data Accessibility section of the article (https://royalsociety.org/journals/ethics-policies/data-sharing-mining/). Reference(s) to datasets should also be included in the reference list of the article with DOIs (where available).

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should also be fully cited and listed in the references.

If you wish to submit your data to Dryad (http://datadryad.org/) and have not already done so you can submit your data via this link
http://datadryad.org/submit?journalID=RSPB&manu=(Document not available), which will take you to your unique entry in the Dryad repository.

If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link.

For more information please see our open data policy http://royalsocietypublishing.org/data-sharing.

Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI. Please try to submit all supplementary material as a single file.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,
Professor Gary Carvalho
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
Thank you for submitting your manuscript to Proceedings B. We have now received two reviews of your manuscript. The reviewers both write that your study is interesting, well-written and addresses an important gap in our understanding of predation risk in group living animals. Both reviewers, however, had concerns that would need to be addressed before the manuscript could be considered for publication in Proceeding B. These concerns are mainly about needing more information about the methods or discussion of how the specific methods used in this study could have influenced the results. The reviewers provide valuable feedback that will improve a future version of the manuscript.

Reviewer(s)' Comments to Author:
Referee: 1
Comments to the Author(s)
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Referee: 2
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Author's Response to Decision Letter for (RSPB-2021-1286.R0)

See Appendix A.

RSPB-2021-1286.R1 (Revision)

Review form: Reviewer 1

Recommendation
Accept as is

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
I am happy with the revision and have no further comments. I especially liked the inset in Fig. 1. Congrats for the excellent paper.

Review form: Reviewer 2

Recommendation
Accept as is

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Excellent

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

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Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
The authors did a thorough job responding to the reviewer comments. The video showing the behavior of the fish is helpful, but it would be great if the authors could combine the fish behavior video with the prey dots. I think that would give readers a much better sense of the experimental setup.
I appreciate that the authors carried out an additional analysis of where the fish were in relation to the prey dots. I'm a bit puzzled by the 2/3 body criteria. Would looking at whether the head was inside/outside the MCP be the appropriate measure? I'm also a bit curious that the authors didn't go the next step and analyze which method works better for attacks form the inside/outside of the group. That just seems logical to me. Given that there was a large % of attacks both in/out of the group in both moving and stationary groups, I assume that this additional analyses might not have yielded important insights. On the other hand, my assumptions about this behavior were somewhat confirmed by this additional data, and I think it would be good to have more info on what exactly is causing this difference in attack behavior on stationary and mobile groups.

Decision letter (RSPB-2021-1286.R1)

23-Aug-2021

Dear Ms Lambert

I am pleased to inform you that your manuscript entitled "The measure of spatial position within groups that best predicts predation risk depends on group movement" has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

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Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,
Professor Gary Carvalho
Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Associate Editor:
Board Member: 1
Comments to Author:
(There are no comments.)

Board Member: 2
Comments to Author:
(There are no comments.)

Appendix A

Dear Editor,

We thank you for giving us the opportunity to revise the manuscript, and the positive and constructive comments made by the reviewers. We have addressed each of these comments in our response below; in most cases we have revised the manuscript to make the changes suggested by the reviewers. Although these have undoubtedly improved the manuscript, the results and take-home messages of the study are unchanged.

Your sincerely,

Poppy Lambert (on behalf of all authors)

Associate Editor

Board Member: 1

Comments to Author:

Thank you for submitting your manuscript to Proceedings B. We have now received two reviews of your manuscript. The reviewers both write that your study is interesting, well-written and addresses an important gap in our understanding of predation risk in group living animals. Both reviewers, however, had concerns that would need to be addressed before the manuscript could be considered for publication in Proceeding B. These concerns are mainly about needing more information about the methods or discussion of how the specific methods used in this study could have influenced the results. The reviewers provide valuable feedback that will improve a future version of the manuscript.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

this is an interesting and well-written manuscript on measures of spatial position of prey depredated by sticklebacks and predation risk. Virtual prey was used in order to manipulate prey and calculate various spatial positions. Movement influenced which measure best predicted predation risk. I have only some minor comments for improvement.

We thank the reviewer for their comments and suggested changes.

Minor comments:

line 71: mention with what sticklebacks were fed.

We have now added to the Methods that the fish were fed defrosted bloodworms before and throughout the experiment (line number 73).

Did they have experience with foraging on Daphnia, which were obviously simulated as prey.

It is unlikely that the fish had experience with Daphnia; although the fish were wild caught, they were caught from a river, and Daphnia are associated with lentic habitats.

Nowhere the reader is informed about the nature of the virtual prey.

We had detailed this at line 55-56, and have added the following information (lines 123-124): "We gave the prey of both types of simulation a small jitter motion, to make them appear more lifelike.". *In addition to the supplementary movies included in the original submission, we have included a new video clip showing the calibration video of trial 5 (with prey visible) followed by the attack of the fish in this trial.*

Please justify the choice of the virtual prey size and movement.

*The size of the prey was determined by the typical size of prey that sticklebacks have adapted to feed on, namely small freshwater invertebrates. The speed of directional movement was similar to the speed of simulated prey movement in Ioannou et al. 2019 (6.8 mm/s). We have summarised in the Methods: "*The size and speed of prey were set to elicit predatory responses from the fish (e.g. as in [Ioannou et al. 2019])" *(lines 122-123).*

To me the movement of the group looks artificial, that is unidirectional with a constantly slow speed. Nevertheless, you generalize the results in terms of movement but the results may strongly depend on the nature of the movement (like speed, direction, variability). Please discuss.

*We completely agree that variables such as speed, direction and variability in these movement parameters may impact the results; in fact, one of the intended 'take-home' messages of the paper was the general principle that the prey's properties of appearance affect which measure of spatial position is the best predictor of predation risk. We apologise that this was not clear enough originally. We have now developed the text in the second paragraph of the Discussion make this clearer and to acknowledge the specific point raised by the reviewer: "*Indeed, our findings are likely to have been different had other aspects of the prey group differed, such as the speed of movement" *(line 288-290).*

Give details of the illumination: how bright was the lightning. This may influence foraging.

We adjusted the lighting to ensure that the prey were visible to the fish on the front screen, not visible to the fish on the rear wall, and that the fish was visible to the camera. We have clarified this in line 90-91. Unfortunately, we did not take measurements of the light levels, which we have not measured and reported in our previous work using the fish predator-virtual prey system. Due to this feedback from the reviewer, we will in the future record light levels in these experiments using a lux meter.

In the videos of the supplement, the virtual prey is seen on the front but also on the back wall. This is not the case in Fig. 1. Did the reflections on the back wall, if visible at all, influence foraging behaviour?

There were no prey visible on the back wall during the trials with the fish, only in the calibration presentations of the prey (without fish being present). This information is now in the text (lines 90-91) so it is clear for the reader. We have also included a new supplementary movie that shows a calibration video followed by these prey being attacked during a trial; in the trial, the prey is not visible on the back wall.

It would be very helpful to the readers if you could visualize the measures listed in Table 1 in a Figure.

We agree; we did not do this in the original submission due to the page limit. We have added such a figure as an inset to figure 1, with an explanation in the figure 1 legend.

Referee: 2

Comments to the Author(s)
The authors tested which methods for measuring an individual's within-group spatial position provided the most predictive power of predation risk in a simulated predation experiment. This is an extremely interesting paper on a topic very near-and-dear to my research interests. Interestingly, the authors found differences in which method works best depending on whether the group was stationary or moving. When groups were stationary, the limited domain of danger was the best predictor (over a broad range of pixel sizes), and when moving, the AoV was the best method (except for N near neighbors over a limited range of pixel sizes). More broadly, individuals in stationary groups were more vulnerable when local prey density was low, while individuals in moving groups were more

vulnerable when close to the "group edge." This paper is well written, the statistic are appropriate, and overall, I really liked this paper. I also hope this paper brings more attention to the importance of how predation risk is measured. Despite a couple of (IMHO) very good papers (Stankowich 2009, Hirsch and Morrell 2011) discussing which measures should be used in different scenarios, I continue to see authors use inappropriate or sub-optimal methods of quantifying spatial position. In addition, the citation rates on these two papers are far lower than I think they should be. I hope that this paper will help change this. I do think that this paper could be revised/rewritten to more accurately reflect the results, and to put the results into better perspective.

The experimental set-up isn't necessarily one I would have used, and I think a different set-up may lead to very different results. I highly suggest that the authors provide additional information/analyses to support their conclusions (details below).

*We agree that different testing conditions, which represent different contexts of predator-prey interactions, will influence the results. This is a major take-home message from the study, as we show that even with all other variables held constant, whether the group is moving or not has a large effect on the results. In response to the other Reviewer's similar comment, we have expanded the text on this in the second paragraph of the Discussion: "*Indeed, our findings are likely to have been different had other aspects of the prey group differed, such as the speed of movement" *(line 288-290; but see also from line 285).*

This experiment is similar to previous lab experiments of predation on simulated prey (Ioannou et al. 2019). The issue with this experimental setup is that the fish are attacking a 2D group of animals from "above."

*We now acknowledge this more explicitly in the Methods: "*Two-dimensional virtual prey were presented to the fish on the front wall of a testing arena, so that the fish's approach was typically from the third dimension, i.e. perpendicular to the 2D spread of the group.*" (line 76 - 78).*

In general, 2D animal groups are on a landscape, and predators either attack them from the same plane (i.e. the old-school lion attacking a cow example), or above (i.e. aerial bird of prey attacking a flock of birds foraging on the ground). The choice of experimental setup should be a really important driver of the results. In the case of terrestrial predators attacking terrestrial prey, and the assumption that predators attack the closest prey (or at a minimum, do not pass by close prey to get to another individual further away), a measure of spatial position relative to the group edge should be the most important determinant of risk. This is the rationale behind the Angle of Vulnerability (AoV) method tested here. In the latter case (aerial predation on terrestrial group), measures of local density could be predicted to be more important (although see Romey et al. 2008). It's also important to note that you are testing the predation behavior of a predator that normally preys on 3D groups (I believe?) with a 2D prey group. What affect does this change in dimensionality have on the predatory behavior of the fish?

We designed the experimental set up, as with our previous studies such as Duffield and Ioannou (2017) and Ioannou et al. (2019), to avoid overly biasing attacks toward the edge of groups (we have now made this explicit in the manuscript, lines 78-79). We agree with the reviewer that if the predator and prey are on the same 2D plane, or the prey are spread in three dimensions, that attacking the edge of the group is much more likely. We note the work of Romenskyy et al. (2020) (line 79-80) which showed that even for a 3D prey group, information about spatial position taken from a 2D plane could predict predation risk.

An interesting observation about this ms is that there are no a priori predictions about if these measures should differ between moving and non-moving groups, and if the authors predict that differences should occur, then which methods should work better in each condition. Following from my points above, I would assume that measures of local density would be better measures of predation risk in this scenario. This may change if the predator is approaching the "group" from one direction (because of the prey group movement). In the case when the fish have to swim over to the prey dots, they could be predicted to prefer targeting close individuals, in which case a measure of "edge" would be the better measure. If stationary groups were mostly targeted by fish attacking directly perpendicular to the prey dots, and if the moving groups were mostly targeted by fish attacking from "outside" the group, the results in this paper make perfect sense. I believe the authors

can test this. What percentage of “attacks” were carried out by fish attacking from “above” vs “outside” the group in each treatment? If the patterns resemble my predictions here, I think the results are quite logical and easy to predict a priori. I would like to see the authors report these numbers, and write/revise the manuscript to reflect the experimental set-up more accurately,

We thank the reviewer for the careful thought given to the set up we used. We have briefly added a prediction at the end of the Introduction regarding the comparison between stationary and moving groups (lines 59-61). Moreover, we have collected additional data from the still images at the moment of each attack and added a new analysis that tests whether the predators were more likely to attack moving groups from outside the group compared to stationary groups (lines 173-181).

Specific comments:
Line 46. And food acquisition! Very important, but not cited. Hirsch 2007 reviews some of the lit on this topic.

We have edited the text here (line 46) and added the reference.

Lines 128-138. Why was this speed chosen? This seems really slow, but it’s hard for me to really picture it in my head.

Please see our response to Reviewer 1 who made a similar comment.

Could the authors provide sample videos with the fish in the video? Could this slow speed be the reason why this study found no evidence of higher predation on front edge individuals when compared with Ioannou et al. 2019?

We have provided an additional supplementary video showing the calibration prey presentation for trial 5, followed by a section of the trial video which corresponds to this presentation of prey and includes the fish’s attack used in the analysis. The speed of prey directional movement in this study (11 mm/s) is quite similar to the speed of prey in Ioannou et al. 2019, so we do not think it likely this is the reason for a difference in findings with regards to predation on front edge individuals.

Lines 252-253. Not just 3D variation in prey groups, but whether the group is 2D or 3D, and what plane the predator is.

We agree, and have developed the text in the Discussion to include this point (lines 296 - 299).

Given that this experiment was done on 2D groups being targeted from above, there is no reason the authors should have predicted higher predation at the front of the group. Increased front edge predation is thought to be caused by 2D moving groups encountering terrestrial sit-and-wait predators. Most previous studies showing this pattern have a very different dimensional setup than the current experiment.

Although we agree with the reviewer that attacks at the front of a moving group are most likely to occur with sit-and-wait predators (such as those used in the Bumann et al. 1997 study), we showed a preference for the front of moving groups in our 2019 study using a very similar set up as in our current paper under consideration. This was one of the novel and interesting findings of this 2019 study, suggesting that greater risk at the front of moving groups is more general than just with sit-and-wait predators. We need to do further investigations to determine under what circumstances the front of moving groups are more at risk, given the contrasting results in the current study compared to our 2019 study.

Lines 264-265. I would argue that the AoV is easily measured in the field when used as a categorical variable. This was explicitly discussed/tested in the original article (Hirsch and Morrell 2011). It’s really odd that the authors bring up the ease of use of certain methods, but then recommend using the LDOD for stationary groups. I would have also liked to have seen the AoV turned into a categorical variable (as in Hirsch and Morrell 2011) and see if the AoV results were better or worse compared to the continuous measure.

Due to space constraints, we have removed the discussion on how easy it would be to measure the different spatial variables in the field, as we think this is the most speculative part of the Discussion and least relevant to our study. We are unsure of the added value of converting any of the continuous measures of spatial position (which most of the measures are) to categorical variables. As we use binomial Generalised Linear Models, statistically it would be unlikely that a categorical version of the predictor variable (the measure of spatial position) could outperform the continuous version. This would also greatly extend the length of the paper, as to do this with minimal bias we would need to categorise every continuous measure of spatial position, with different numbers of categories for each, and different thresholds used to determine the categories.