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Inferring collective behaviour from a fossilized fish shoal

Nobuaki Mizumoto, Shinya Miyata and Stephen C. Pratt

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1st revised submission:	15 April 2019
2nd revised submission:	8 May 2019
Final acceptance:	9 May 2019

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

Review History

RSPB-2019-0280.R0 (Original submission)

Review form: Reviewer 1

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.
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 found this paper both fascinating and very well written. It's an enormous - some would say insuperable - challenge to infer movement, let alone collective movement, from the fossil record. While accepting that the authors have taken considerable care to examine alternative explanations for their observation, and produce a plausible argument that it is an example of collective movement, it is impossible to be certain, based on the available evidence. Given that no historical data of this kind could ever fully satisfy all objections, it then comes down to a judgement of whether any such data can be accepted at face value. Some people would take a hard line and say 'never', while others would allow it, if it is cautiously interpreted. While I appreciate the scientific rigour that underlies the former point of view, and accept that this is likely to polarise opinion, I think it would be unfortunate to exclude this interesting work from the literature. Overall, I recommend acceptance, but I do think that the authors should be more cautious in their claims, acknowledging the reasonable doubt that remains even after their painstaking evaluation.

The validity of the paper's findings rests on a number of assumptions:

- that the fish were preserved in some instantaneous catastrophic event. This seems incredibly unlikely but then again, I'm no expert in fossil formation. Is it feasible to gather some additional geological knowledge relating to the fossiliferous rocks? Why is this impossible (line 221)?

- that the fish were moving in a 2D shoal. This is a fundamental assumption of the analysis, however it's unusual even for shoals that are described in such terms to be entirely and uniformly compressed on a horizontal plane. This might be why the inter-individual distances are so small - because a 3D shoal was compressed by some catastrophic event - which would result in the appearance of such small inter-individual distances.

- that the 'aggregation' was not caused by a single catastrophic event, but rather represents an accumulation of bodies over a short - but not simultaneous - time scale. This is also a potential explanation for the very small near-neighbour distances. The authors do a reasonable job of interrogating this possibility, and that the pattern is caused by what they call a taphonomic process. Large-scale fish die-offs that I have seen tend to show patterns of alignment, particularly in flowing water. I don't wish to discount the authors' arguments in this respect, however it is equally possible that an accumulation of bodies was preserved by the same kinds of instantaneous events that are invoked to explain the capture of a living shoal, before disintegration occurred (line 205 - 209).

- this is really a minor point, but there's an assumption that the fish were moving at uniform speed, as suggested by the manipulations to their position along the heading direction (line 103). Generally, fish move at a speed that is proportional to their body length, so a relative measure might provide more information, especially since there is an unusual range of sizes within this group.

I was surprised to see that there was no trend for larger fish to be found at the front of the shoal - in polarised shoals of extant, free-ranging fish, this is almost universally the case.

The legend for Figure 3d reads 'distane'

Review form: Reviewer 2

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?
Acceptable

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
Yes

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
Please see my detailed comments in the attached file (See Appendix A).

Decision letter (RSPB-2019-0280.R0)

18-Mar-2019

Dear Dr Mizumoto:

I am writing to inform you that your manuscript RSPB-2019-0280 entitled "Inferring collective behavior from a fossilized fish shoal" has, in its current form, been rejected for publication in Proceedings B.

This action has been taken on the advice of referees, who have recommended that substantial revisions are necessary. With this in mind we would be happy to consider a resubmission, provided the comments of the referees are fully addressed. However please note that this is not a provisional acceptance.

The resubmission will be treated as a new manuscript. However, we will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

Please find below the comments made by the referees, not including confidential reports to the Editor, which I hope you will find useful. If you do choose to resubmit your manuscript, please upload the following:

1) A 'response to referees' document including details of how you have responded to the comments, and the adjustments you have made.
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Sincerely,
Proceedings B
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:

Thank you for submitting this very interesting research. Two reviewers has now evaluated the manuscript and both agree this is a novel and exciting piece of work. Both also have a number of recommendations for manuscript improvement and it is believed that the authors should be able to accomplish these tasks. In particular, the reviewers would like to see the connection between the empirical data and simulation strengthened, better support for the underlying assumptions, and some caution in terms of broad overarching statements/interpretations. If the authors are able to address these points in the paper, it work is expect to make a substantial and novel addition to the literature.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
I found this paper both fascinating and very well written. It's an enormous - some would say insuperable - challenge to infer movement, let alone collective movement, from the fossil record. While accepting that the authors have taken considerable care to examine alternative explanations for their observation, and produce a plausible argument that it is an example of collective movement, it is impossible to be certain, based on the available evidence. Given that no historical data of this kind could ever fully satisfy all objections, it then comes down to a judgement of whether any such data can be accepted at face value. Some people would take a hard line and say 'never', while others would allow it, if it is cautiously interpreted. While I appreciate the scientific rigour that underlies the former point of view, and accept that this is likely to polarise opinion, I think it would be unfortunate to exclude this interesting work from the literature. Overall, I recommend acceptance, but I do think that the authors should be more cautious in their claims, acknowledging the reasonable doubt that remains even after their painstaking evaluation.

The validity of the paper's findings rests on a number of assumptions:

- that the fish were preserved in some instantaneous catastrophic event. This seems incredibly unlikely but then again, I'm no expert in fossil formation. Is it feasible to gather some additional geological knowledge relating to the fossiliferous rocks? Why is this impossible (line 221)?

- that the fish were moving in a 2D shoal. This is a fundamental assumption of the analysis, however it's unusual even for shoals that are described in such terms to be entirely and uniformly compressed on a horizontal plane. This might be why the inter-individual distances are so small - because a 3D shoal was compressed by some catastrophic event - which would result in the appearance of such small inter-individual distances.

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Generally, fish move at a speed that is proportional to their body length, so a relative measure might provide more information, especially since there is an unusual range of sizes within this group.

I was surprised to see that there was no trend for larger fish to be found at the front of the shoal - in polarised shoals of extant, free-ranging fish, this is almost universally the case.

The legend for Figure 3d reads 'distane'

Referee: 2

Comments to the Author(s)
Please see my detailed comments in the attached file.

Author's Response to Decision Letter for (RSPB-2019-0280.R0)

See Appendix B.

RSPB-2019-0891.R0

Review form: Reviewer 1

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

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
As previously, I think this is a fascinating paper and am satisfied with the changes undertaken by the authors. Doubts remain, but these are acknowledged. Looking forward to seeing it in print.

Review form: Reviewer 2

Recommendation
Accept with minor revision (please list 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?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
Yes

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 think that the authors have done a good job addressing both my comments and referee 1's comments in their revised manuscript, and suggest that this very interesting and novel article should be published. In working through the revised manuscript, I had the following thoughts that the authors might consider if they have the opportunity to make any more small revisions to the article (see the attached pdf).

Decision letter (RSPB-2019-0891.R0)

03-May-2019

Dear Dr Mizumoto

I am pleased to inform you that your manuscript RSPB-2019-0891 entitled "Inferring collective behavior from a fossilized fish shoal" has been accepted for publication in Proceedings B.

The referee(s) have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to the referee(s)' comments and revise your manuscript. Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript within 7 days. If you do not think you will be able to meet this date please let us know.

To revise your manuscript, log into https://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. You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referee(s) and upload a file "Response to Referees". You can use this to document any changes you make to the original 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.

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3) Electronic supplementary material: this should be contained in a separate file and where possible, all ESM should be combined into a single file. 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.

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4) A media summary: a short non-technical summary (up to 100 words) of the key findings/importance of your manuscript.

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It is a condition of publication that data supporting your paper are made available either in the electronic supplementary material or through an appropriate repository.

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should be fully cited. To ensure archived data are available to readers, authors should include a ‘data accessibility’ section immediately after the acknowledgements section. This should list the database and accession number for all data from the article that has been made publicly available, for instance:
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Once again, thank you for submitting your manuscript to Proceedings B and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Sincerely,

Proceedings B
mailto: proceedingsb@royalsociety.org

Associate Editor
Comments to Author:
Both reviewers agree this manuscript is a great contribution, with only a few minor edits (see attached PDF). Please make sure data needed to replicate the study are made available as supplementary material or uploaded to Dryad.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s).
As previously, I think this is a fascinating paper and am satisfied with the changes undertaken by the authors. Doubts remain, but these are acknowledged. Looking forward to seeing it in print.

Referee: 2

Comments to the Author(s).
I think that the authors have done a good job addressing both my comments and referee 1's comments in their revised manuscript, and suggest that this very interesting and novel article should be published. In working through the revised manuscript, I had the following thoughts that the authors might consider if they have the opportunity to make any more small revisions to the article (see the attached pdf).

Author's Response to Decision Letter for (RSPB-2019-0891.R0)

See Appendix C.

Decision letter (RSPB-2019-0891.R1)

09-May-2019

Dear Dr Mizumoto

I am pleased to inform you that your manuscript entitled "Inferring collective behavior from a fossilized fish shoal" 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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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,

Proceedings B
mailto: proceedingsb@royalsociety.org

Appendix A

Inferring collective behavior from a fossilized fish shoal

The authors use data on the relative positions and orientations of a fossilized group of fish, *Erismatopterus levatus*, to infer that these relative positions and orientations are consistent with individuals moving to avoid collisions at short range (a repulsion effect) and an attraction to individuals outside the range of the repulsion effect. A number of calculations are done to support the hypothesis that such interactions were genuinely present, and to contrast with cases where no such interactions are present. Complimentary calculations are performed with a self-propelled particle model to illustrate that group formations qualitatively similar to that observed in the fossil can emerge when individuals apply interaction rules to avoid groupmates at short range, and align with and move towards group mates over a finite range (outside of the avoidance zone/zone of repulsion).

I don't know of any other study that has attempted this sort of analysis of fossil records, and I think the methods of direct analysis of the data seem sound, making this a novel and exciting study. In fact, I think that the authors may have even stronger evidence that the positioning and orientation of individuals arises due to some sort of inter-individual interactions than they realise (based on discussions in earlier papers on extracting interaction rules from animal movement data, particularly work by Ballerini et al. (2008) (Interaction ruling animal collective behavior depends on topological rather than metric distance: evidence from a field study, *PNAS* **105**(4):1232-1237)). I think the weakest element of the paper is the connection between the self-propelled particle model work and the direct analysis. I also think that perhaps more care should be made in making statements like "we infer the behavioral rules", which could be understood as *the* one and only set of possible rules, when in fact there could be multiple behavioural rules that lead to the formation observed in the fossil (with the authors inferring and discussing in detail one such possible (and very plausible) set of rules).

This paper made me think about the interactions thought to drive collective motion, and how some of the hypothesised interactions (repulsion- and attraction-like rules) seem to be consistent across species, including the fossilised *Erismatopterus levatus,* a great deal. Perhaps there is a degree of universality in these types of rules? I enjoyed reviewing this paper, and sorry for the late submission of my review. My recommendation is acceptance conditional on major revisions, with the most important revisions trying to strengthen the connection between simulation and empirical results. I have referenced a number of papers in my suggestions to the authors below, which may be helpful to the authors in their revisions, but I don't expect that the authors necessarily reference these papers in their revision, unless they think it is relevant.

Suggestions

Abstract

Line 34. It might be safer to write "we infer possible behavioral rules" rather than "we infer the behavioral rules" which might imply you've identified that there is one set of rules only that would produce the observed group structure in the fossil.

Introduction

I think it might be better to make the first two sentences of the paragraph less absolute for the following reasons.

Lines 44-45. It is a strong and reasonable hypothesis that coordinated collective motion results from local interactions among group members, and this hypothesis is supported by a number of theoretical/simulation studies, but has a direct causal relationship between local interactions and emergent group level movement patterns of movement been established for real animal groups?

Lines 45-46. The form of the interaction rules used in theoretical studies often includes some combination of short range collision avoidance rules, and alignment and attraction rules that apply over some spatial or topological range. Analysis of trajectory data like those in the studies by Katz et al. (2011) and Herbert-Read et al. (2011) suggest that the basic principles of these rules seem to apply for the two species of fish studied, although differing in detail in how the animals avoid collisions and exhibit attraction-like behaviour compared to model based rules. For example, collision avoidance in the model studied by Couzin et al. (2002) and the model that you use is controlled through changes in direction, whereas it seems that golden shiners use a combination of changes in both speed and direction to avoid collisions (Katz et al. (2011)), and eastern mosquitofish rely on changes in speed to avoid collisions at short range (Herbert-Read et al. (2011)). Subsequent studies suggest that similar (but not identical in detail) behaviour can be seen for guppies (Herbert-Read et al. (2017) How predation shapes the social interactions of shoaling fish, *Proc R Soc B* **284**:20171126) and x-ray tetras (Schaerf et al. (2017) The effects of external cues on individual and collective behavior of shoaling fish, *Sci Adv* **3**:e1603201) for example, but I think it is a long leap to make to suggest that all animals follow the three basic rules of thumb often used in models when coordinating collective motion (even though these rules are a very reasonable hypothesis).

Lines 66-68. I think it might be better to state that you've "inferred possible behavioral rules…" rather than "the behavioral rules", to allow for the fact that the group level pattern seen in the fossil could have arisen from a number of different combinations of behavioural rules. For example, it has been shown that parallel group motion can emerge when individuals only use an alignment based interaction rule to adjust their velocity (Vicsek et al. (1995) Novel type of phase transition in a system of self-driven particles, *Physical Review Letters*, **75**(6):1226-1229), when individuals make use of a combination of repulsion, orientation and attraction interactions (Couzin et al. (2002)), when individuals make use of a combination of repulsion and attraction interactions (D'Orsogna et al. (2006) Self-propelled particles with soft-core interactions: patterns, stability and collapse, *Physical Review Letters* **96**:104302) and when individuals make use of only an attraction-type interaction rule (Strömbom (2011) Collective motion from local attraction, *Journal of Theoretical Biology* **283**:145-151).

Figure 1. The arrowhead pointing in the facing direction of the focal individual is missing from panel C, and neighbour is spelt incorrectly on the vertical axis label on panel D. Also, even though you have relatively few data points to construct panel C, I agree with your observation that nearest neighbours were more frequently laterally positioned as noted on lines 164-165. Given that your graph also seems to have some structure (with many nearest neighbour occupying an annular region from about 2 to 8mm), the greater frequency of nearest neighbours to the sides compared to the front and back could be evidence in itself of the structure of the group arising from some form of local interaction. Ballerini et al. (2008) (Interaction ruling animal collective behavior depends on topological rather than metric

distance: evidence from a field study, *PNAS* **105**(4):1232-1237) used an argument that interactions in a moving animal group could lead to anisotropy in frequency plots of near neighbour positions to infer that the starlings that they observed were interacting with up to at least 6 or 7 of their nearest neighbours. Since your graph has both structure and anisotropy, perhaps you could point to this as evidence of there being some sort of local interaction between first nearest neighbours (with reference to Ballerini et al. (2008))? (But also note the discussion in the SI for Ballerini et al. (2008), in the section on "The connection between structure and interaction" where it is noted that explicit interactions can still result in isotropic spatial structure of group members.)

Data Analysis

Lines 92-93. I think you should state explicitly what criteria was used to define when individuals were apart from the main aggregation (for example, were these individuals more than a certain number of body lengths away from any other individual in the group)?

Line 95. Replace "… this heading direction vector…" with "… the length of the heading direction vector…" or "… the magnitude of the heading direction vector…".

Line 97. Replace "… center of these two lines…" with "… intersection of these two lines…".

Lines 102-105. I think some more explicit details about this process, and some re-wording, are needed. In particular, did you extrapolate the position of one fish at a time, and determine if it moved towards or away from its groupmates based on their static positions in the fossil? Or did you move all individuals at the same time, and compare all extrapolated positions post move (or something else)? Also, it might be best to re-iterate that the comparisons are made between nearest neighbours (rather than just "neighbouring individuals") on line 104.

Lines 116-117. The reference to "(also see main text)" is in the main text!

Simulations

Line 135. Why did you choose to do the simulations in a periodic domain (in both spatial dimensions) rather than an unbounded domain? In extreme cases, such as a group becoming very elongated in one spatial dimension, individuals at the front of the group may end up interacting directly with individuals at the rear of the group (and vice versa) due to the doubly periodic domain.

Lines 137-138. The second behavioural rule has two separate additive components, an orientation term and an attraction term (as noted in the equation on line 145). In previous work (such as Couzin et al. (2002)), orientation and attraction effects have operated over separate zones, and have been treated as potentially different rules, before being combined in the same form of equation that you state on line 145. This leaves me unsure whether interactions within your second larger zone should be noted as a single rule, or a combination of rules (even though the overall effect is summarised by a single equation). At other points in the text (for example, on line 147), the zone where $r_z < r < r_a$ is referred to as an attraction zone, whereas it is explicitly a zone of both alignment/orientation and attraction; please take care not to refer to this model zone as just a zone of attraction throughout the text, because that may not be entirely accurate. Also, your analysis of potential movements in the group does seem to suggest the presence of repulsion and attraction effects, but nothing explicit about alignment (with theory suggesting alignment across a group can occur with or without an explicit alignment rule); why did you choose to include an explicit alignment term/rule in your model?

Lines 133-157. What rules did the model fish use to adjust their speed (if any)? You note on lines 152-153 that "Once its direction was determined, the fish moved with a speed of $\left|v_i\left(t+\Delta t\right)\right|$, which was limited to a range given in Table S1.", but this sentence effectively just says that the speed of the fish was its speed. Were changes in speed governed by particular rules or equations, or chosen randomly over the given range of 3-7 units, or something else (please provide details)?

Table S1. (In the SI.) What lead you to use these particular parameter values?

Results and Discussion

Lines 165-166. I think that references to papers 16-18 here might not be quite correct. Fig 5a. of reference 16 shows distributions of first, second and third nearest neighbours as a function of the distance to these neighbours, but not the sort of detail about laterally positioned neighbours that is shown in your overhead frequency distribution plot for nearest neighbours in your Fig. 1C. Neither Herbert-Read et al. (2011) nor Calovi et al. (2017) present graphs of relative frequency as a function of relative neighbour coordinates or distances. As a point of reference, the following papers present plots similar to your larger plot in Fig. 1C for a variety of species (although some of these plots are constructed based on the relative positions of all neighbours, not just nearest neighbours, as noted):

Lukeman et al. (2010) Inferring individual rules from collective behavior, *PNAS* **107**(28):12576-12580 (Fig 2. A for surf scoters, plot generated using all neighbours, with greatest frequencies occurring in front and behind the focal individual).

Katz et al. (2011) (as already in your reference list, Fig. 1B for pairs of golden shiners, again with greatest frequencies occurring in front and behind the focal individual).

Schaerf et al. (2017) The effects of external cues on individual and collective behavior of shoaling fish, *Science Advances* **3**:e1603201 (Fig. 6 for x-ray tetras, plot generated using all neighbours, with greatest frequencies occurring to the sides of the focal individual, as is the case with your nearest neighbour plot).

Ward et al. (2017) Local interactions and global properties of wild, free-ranging stickleback shoals, *Royal Society Open Science* **4**:170043 (Fig. 5 (a) for three-spine sticklebacks, plot generated using all neighbours for wild groups of at least 10 fish, with greatest frequencies occurring to the sides of the focal individual).

Raven et al. (2017) The role of biotic and abiotic cues in stimulating aggregation by larval cane toads (*Rhinella marina*), *Ethology* **123**:724-735 (Figure 2 for cane toad tadpole aggregations, with greatest frequencies occurring to the sides of the focal individual).

Herbert-Read et al. (2017) Anthropogenic noise pollution from pile-driving disrupts the structure and dynamics of fish shoals, *Proceedings of the Royal Society B* **284**:20171627 (Fig. 1 (b) for juvenile seabass, plot generated using nearest neighbours, with greatest frequencies occurring to the sides of the focal individual (equivalent to your results)).

Lines 179-180. I think you need to be careful with your wording here, the way the sentence is written makes it seem like it's been established that the main rules of interaction for all extant fish are repulsion and attraction-like rules. Based on published analysis, it does seem that golden shiners and eastern mosquitofish make primarily repulsion and attraction based adjustments to their velocity (Katz et al. 2011 and Herbert-Read et al. 2011), but explicit analysis of another species (guppies) suggested that there may also be a tendency to align with other group members (see Fig. 5 (b) and associated discussion in Herbert-Read et al. (2017) How predation shapes the social interactions of shoaling fish, *Proc R Soc B* **284**:20171126). There is also evidence that there may be a tendency to align in groups of x-ray tetras (Fig 7. in Schaerf et al. (2017) The effects of external cues on individual and collective behavior of shoaling fish, *Science Advances* **3**:e1603201) and three-spine sticklebacks (Fig 5. (b) in Ward et al. (2017) Local interactions and global properties of wild, free-ranging stickleback shoals, *Royal Society Open Science* **4**:170043), but neither of these studies perform the explicit analysis used by Katz et al. 2011, Herbert-Read et al. 2011 or Herbert-Read et al. 2017 to further explore if there really is an alignment interaction occurring or not.

Line 184. Maybe it would be better to write "tend to attack" rather than "are supposed to attack"?

Lines 186-187. The polarisation is not "the absolute value of the mean individual heading direction", and the stated formula is also incorrect. One way determine the polarisation is to construct unit vectors in the facing directions of each of your fish, which could be denoted v_i as you have used. Then, to determine the polarisation: add all the individual unit vectors, determine the magnitude/length of the resultant vector (from the sum of individual unit vectors), and then divide the length of the resultant vector by the number of group members, N. Using your notation, the formula for the polarisation could then be written as:

$\rho = \frac{1}{N}\left|\sum_{i=1}^{N} v_i\right|$ (the error in your formula was just a minus sign in front of the sum).

Lines 190-191 and 216-217. Perhaps it is not necessary to remove the individuals with the almost opposite headings to that of the bulk of the group from your analysis? A polarisation of 0.902 is already quite high for a dynamic fish shoal, and it seems plausible to me that the orientations of the fish may not have been modified.

Line 221. The referencing style for ref 23 does not seem consistent.

Lines 235-250. This is the part of the study that I found least convincing, and perhaps the connection between the empirical and simulation analysis could be strengthened. First, I think that your choices of using a set of 1000 simulations, and using data from the 10000th time step (when transient behaviour in the model has likely disappeared) to compare with your data are completely reasonable. I also think that your comparison of the length to width ratio of the fossil and simulated groups is reasonable.

What I'm not sure about is your choice to include an explicit alignment/orientation rule in your model, when your data analysis picks out just repulsion and attraction effects. It might be better (or more convincing at least?) to start out with a model that only has explicit repulsion and attraction effects. As I noted earlier, one such model is that described by

(D'Orsogna et al. (2006) Self-propelled particles with soft-core interactions: patterns, stability and collapse, *Physical Review Letters* **96**:104302), with another helpful description of the model in (Cañizo et al. (2010) Collective behavior of animals: swarming and complex patterns, *Arbor* **186**:1035-1049). The model is a differential equation model, and the ranges over which repulsion and attraction effects work are not as easy to interpret as in the zonal model of Couzin et al. (2002) (just by looking at the equations), but it is possible for parallel motion to emerge from just repulsion and attraction in the model (which seems better aligned with your empirical work). If you did choose to explore what happens with the D'Orsogna model, then (using the notation and model formulation from Cañizo et al. (2010)) one set of parameters that can lead to parallel group motion (after about 5000 time steps) is $\alpha = 1$, $\beta = 1$, $C_A = 100$, $C_R = 50$, $l_A = 50$, $l_R = 5$ with a particle speed of 5 units per unit time. I'd also suggest using an explicit scheme for doing the time-stepping/time-integration for the system (like Euler's method, or a second or fourth order Runge-Kutta method with time steps, $\Delta t = 0.1$), as opposed to an implicit method or package solver (otherwise the calculations will take a huge amount of time).

I also think that you need to explain somewhere in your text why you chose the particular model parameter values that you used (as per my comment in the simulations section). It might be worthwhile for you to look at the approach that Lukeman et al. (2010) used to try to match model output with empirical results as well; this includes a systematic approach to identifying what types of interactions should be included (or not).

Lines 246-247, and Fig 3. D. One of the key features from your equivalent plot for the fossil data was the more frequent appearance of nearest neighbours to the sides of an individual (compared to the front and back). However, your simulation results show greater frequencies of nearest neighbours to the front and back of individuals as compared to the sides, which might suggest that your model might not be quite right in detail (perhaps due to parameter choices within your model, or the form of the model). I think that if you were able to adjust your model to give results consistent with greater frequencies of nearest neighbours in lateral positions it would make the connection between model and simulation more convincing. (I know it may be hard to do this though, so if you cannot generate the same structure in relative positions of nearest neighbours with your model, you could still discuss the differences between simulated and empirical data and what the difficulties might be in getting a simulation to match reality in this case.)

Also, note that "Distance" is spelt incorrectly on the vertical and horizontal axis labels on Fig. 3.

Lines 269-270 and 272-273. These statements leapt out at me as being a bit too strong. I think you need more evidence to convince a reader that the fish were shoaling solely to avoid predators (although this is a reasonable possibility), and that the predation pressure was high (rather than just an existing pressure).

Lines 281-285. Repulsion and attraction rules also seem to appear in the behaviour of guppies (another species in the Cyprinodontiformes order, analysis in Herbert-Read et al. (2017) How predation shapes the social interactions of shoaling fish, *Proc R Soc B* **284**:20171126), and x-ray tetras (from the Characiformes order, analysis in Schaerf et al. (2017) The effects of external cues on individual and collective behavior of shoaling fish, *Science Advances*

3:e1603201). It might bolster your discussion to include these, as you then have five species across three different orders exhibiting repulsion and attraction consistent behaviour, in addition to *E. levatus*. It is also very interesting that the repulsion/attraction type rules of interaction are consistent across these species (even if the details of how repulsion and attraction work might differ between species).

Appendix B

Response to Referees

Referee1:

I found this paper both fascinating and very well written. It's an enormous - some would say insuperable - challenge to infer movement, let alone collective movement, from the fossil record. While accepting that the authors have taken considerable care to examine alternative explanations for their observation, and produce a plausible argument that it is an example of collective movement, it is impossible to be certain, based on the available evidence. Given that no historical data of this kind could ever fully satisfy all objections, it then comes down to a judgement of whether any such data can be accepted at face value. Some people would take a hard line and say 'never', while others would allow it, if it is cautiously interpreted. While I appreciate the scientific rigour that underlies the former point of view, and accept that this is likely to polarise opinion, I think it would be unfortunate to exclude this interesting work from the literature. Overall, I recommend acceptance, but I do think that the authors should be more cautious in their claims, acknowledging the reasonable doubt that remains even after their painstaking evaluation.

Reply: Thank you for your encouraging comments. According to your comments, we revised the manuscript to explain our assumption in details and to acknowledge the limitations of our study. Please see below.

The validity of the paper's findings rests on a number of assumptions:

Comment 1: - *that the fish were preserved in some instantaneous catastrophic event. This seems incredibly unlikely but then again, I'm no expert in fossil formation. Is it feasible to gather some additional geological knowledge relating to the fossiliferous rocks? Why is this impossible (line 221)?*

Reply: In the revised manuscript, we have added to the discussion based on geological information obtained from the specimen (P7L260–268). However, we could not obtain any evidence from the specimen to support the occurrence of an instantaneous catastrophic event. This is because the museum specimen consists only of a very thin slab, giving no information about the overlying or underlying layers or the entire bedding structures (P7L252–257). In the abstract, we now clarify the limitation of this study; it remains unclear how the pattern of a fish shoal was preserved in the fossil (P1L39).

Comment 2: - *that the fish were moving in a 2D shoal. This is a fundamental assumption of the analysis, however it's unusual even for shoals that are described in such terms to be entirely and uniformly compressed on a horizontal plane. This might be why the inter-individual distances are so small - because a 3D shoal was compressed by some catastrophic event - which would result in the appearance of such small inter-individual distances.*

Reply: In the revised manuscript, we have clarified that the actual fish shoal moves in three-dimensional space, while fossilized fish were distributed on the two-dimensional surface on the slab

(P3L103–P4L111). As we analyzed the positions and directions of individuals two-dimensionally, we may underestimate the distance between neighboring individuals. But we expect that the relationship between neighboring individuals should be qualitatively robust given that vertical distances are often smaller than frontal or horizontal distances. We also mentioned that the observed distances between nearest individuals were relatively smaller than those obtained by the observations of extant fish, probably because three-dimensional structures were compressed onto two dimensions during fossilization (P6L197–L199).

Comment 3: - *that the 'aggregation' was not caused by a single catastrophic event, but rather represents an accumulation of bodies over a short - but not simultaneous - time scale. This is also a potential explanation for the very small near-neighbour distances. The authors do a reasonable job of interrogating this possibility, and that the pattern is caused by what they call a taphonomic process. Large-scale fish die-offs that I have seen tend to show patterns of alignment, particularly in flowing water. I don't wish to discount the authors' arguments in this respect, however it is equally possible that an accumulation of bodies was preserved by the same kinds of instantaneous events that are invoked to explain the capture of a living shoal, before disintegration occurred (line 205 - 209).*

Reply: Thank you for this comment. In the revised manuscript, we acknowledge that we cannot completely exclude the possibility that the aggregation of fish was caused by an accumulation of dead bodies over a short time, even with our results supporting that the fish distribution on the slab should reflect fish behavior (P7L268–L271). Thus we now note that a limitation of this study is uncertainty about how the pattern of a fish shoal was preserved in the fossil (P1L39).

Comment 4: - *this is really a minor point, but there's an assumption that the fish were moving at uniform speed, as suggested by the manipulations to their position along the heading direction (line 103). Generally, fish move at a speed that is proportional to their body length, so a relative measure might provide more information, especially since there is an unusual range of sizes within this group.*

Reply: According to the comment, we re-analyzed the data with moving distance proportional to their body length (0.0001 × body-length / average-body-length mm), which did not change the results qualitatively (P4L113–L115, P6L206, Fig. 1D).

Comment 5: *I was surprised to see that there was no trend for larger fish to be found at the front of the shoal - in polarised shoals of extant, free-ranging fish, this is almost universally the case.*

Reply: In the revised manuscript, we mentioned that size sorting is commonly observed in extant fish shoals (P6L233–L234).

Comment 6: *The legend for Figure 3d reads 'distane'*

Reply: Thank you for pointing out the typo. We corrected Fig. 3D.

Referee2:

The authors use data on the relative positions and orientations of a fossilized group of fish, Erismatopterus levatus, to infer that these relative positions and orientations are consistent with individuals moving to avoid collisions at short range (a repulsion effect) and an attraction to individuals outside the range of the repulsion effect. A number of calculations are done to support the hypothesis that such interactions were genuinely present, and to contrast with cases where no such interactions are present. Complimentary calculations are performed with a self-propelled particle model to illustrate that group formations qualitatively similar to that observed in the fossil can emerge when individuals apply interaction rules to avoid groupmates at short range, and align with and move towards group mates over a finite range (outside of the avoidance zone/zone of repulsion). I don't know of any other study that has attempted this sort of analysis of fossil records, and I think the methods of direct analysis of the data seem sound, making this a novel and exciting study. In fact, I think that the authors may have even stronger evidence that the positioning and orientation of individuals arises due to some sort of inter-individual interactions than they realise (based on discussions in earlier papers on extracting interaction rules from animal movement data, particularly work by Ballerini et al. (2008) (Interaction ruling animal collective behavior depends on topological rather than metric distance: evidence from a field study, PNAS 105(4):1232-1237)). I think the weakest element of the paper is the connection between the self-propelled particle model work and the direct analysis. I also think that perhaps more care should be made in making statements like "we infer the behavioral rules", which could be understood as the one and only set of possible rules, when in fact there could be multiple behavioural rules that lead to the formation observed in the fossil (with the authors inferring and discussing in detail one such possible (and very plausible) set of rules). This paper made me think about the interactions thought to drive collective motion, and how some of the hypothesised interactions (repulsion- and attraction-like rules) seem to be consistent across species, including the fossilised Erismatopterus levatus, a great deal. Perhaps there is a degree of universality in these types of rules? I enjoyed reviewing this paper, and sorry for the late submission of my review. My recommendation is acceptance conditional on major revisions, with the most important revisions trying to strengthen the connection between simulation and empirical results. I have referenced a number of papers in my suggestions to the authors below, which may be helpful to the authors in their revisions, but I don't expect that the authors necessarily reference these papers in their revision, unless they think it is relevant.

Reply: Thank you for your very detailed comments and a lot of helpful information. We revised the manuscript according to your comments. Please see below.

Suggestions

Abstract

Comment 1: *Line 34. It might be safer to write "we infer possible behavioral rules" rather than "we infer the behavioral rules" which might imply you've identified that there is one set of rules only that would produce the observed group structure in the fossil.*

Reply: We revised this part accordingly (P1L34).

Introduction

I think it might be better to make the first two sentences of the paragraph less absolute for the following reasons.

Comment 2: *Lines 44-45. It is a strong and reasonable hypothesis that coordinated collective motion results from local interactions among group members, and this hypothesis is supported by a number of theoretical/simulation studies, but has a direct causal relationship between local interactions and emergent group level movement patterns of movement been established for real animal groups?*

Reply: We rephrased the sentence to avoid an overly conclusive description (P2L45–L46).

Comment 3: *Lines 45-46. The form of the interaction rules used in theoretical studies often includes some combination of short range collision avoidance rules, and alignment and attraction rules that apply over some spatial or topological range. Analysis of trajectory data like those in the studies by Katz et al. (2011) and Herbert-Read et al. (2011) suggest that the basic principles of these rules seem to apply for the two species of fish studied, although differing in detail in how the animals avoid collisions and exhibit attraction-like behaviour compared to model based rules. For example, collision avoidance in the model studied by Couzin et al. (2002) and the model that you use is controlled through changes in direction, whereas it seems that golden shiners use a combination of changes in both speed and direction to avoid collisions (Katz et al. (2011)), and eastern mosquitofish rely on changes in speed to avoid collisions at short range (Herbert-Read et al. (2011)). Subsequent studies suggest that similar (but not identical in detail) behaviour can be seen for guppies (Herbert-Read et al. (2017) How predation shapes the social interactions of shoaling fish, Proc R Soc B 284:20171126) and xray tetras (Schaerf et al. (2017) The effects of external cues on individual and collective behavior of shoaling fish, Sci Adv 3:e1603201) for example, but I think it is a long leap to make to suggest that all animals follow the three basic rules of thumb often used in models when coordinating collective motion (even though these rules are a very reasonable hypothesis).*

Reply: Following the comment, we rephrased the sentence to remove the implication that short range repulsion and long range alignment and/or attraction rules are the only mechanisms of coordinate collective motion (P2L46–L48).

Comment 4: *Lines 66-68. I think it might be better to state that you've "inferred possible behavioral rules…" rather than "the behavioral rules", to allow for the fact that the group level pattern seen in the fossil could have arisen from a number of different combinations of behavioural rules. For example,* *it has been shown that parallel group motion can emerge when individuals only use an alignment based interaction rule to adjust their velocity (Vicsek et al. (1995) Novel type of phase transition in a system of self-driven particles, Physical Review Letters, 75(6):1226-1229), when individuals make use of a combination of repulsion, orientation and attraction interactions (Couzin et al. (2002)), when individuals make use of a combination of repulsion and attraction interactions (D'Orsogna et al. (2006) Self-propelled particles with soft-core interactions: patterns, stability and collapse, Physical Review Letters 96:104302) and when individuals make use of only an attraction-type interaction rule (Strömbom (2011) Collective motion from local attraction, Journal of Theoretical Biology 283:145-151).*

Reply: Thank you for this information. We have accordingly changed the wording to "inferred possible behavioral rules" (P2L67-L68).

Comment 5: *Figure 1. The arrowhead pointing in the facing direction of the focal individual is missing from panel C, and neighbour is spelt incorrectly on the vertical axis label on panel D. Also, even though you have relatively few data points to construct panel C, I agree with your observation that nearest neighbours were more frequently laterally positioned as noted on lines 164-165. Given that your graph also seems to have some structure (with many nearest neighbour occupying an annular region from about 2 to 8mm), the greater frequency of nearest neighbours to the sides compared to the front and back could be evidence in itself of the structure of the group arising from some form of local interaction. Ballerini et al. (2008) (Interaction ruling animal collective behavior depends on topological rather than metric distance: evidence from a field study, PNAS 105(4):1232-1237) used an argument that interactions in a moving animal group could lead to anisotropy in frequency plots of near neighbour positions to infer that the starlings that they observed were interacting with up to at least 6 or 7 of their nearest neighbours. Since your graph has both structure and anisotropy, perhaps you could point to this as evidence of there being some sort of local interaction between first nearest neighbours (with reference to Ballerini et al. (2008))? (But also note the discussion in the SI for Ballerini et al. (2008), in the section on "The connection between structure and interaction" where it is noted that explicit interactions can still result in isotropic spatial structure of group members.)*

Reply: First, we corrected Fig. 1. Second, we added a sentence relating to the anisotropy structures observed in the distribution of the distance to the nearest neighbors with a reference to Ballerini et al. 2008 (P5L193–P6L197). As discussed in this study, this anisotropy in the structures is probably caused by the lateral visual field and elongated body shape along the direction of motion.

Data Analysis

Comment 6: *Lines 92-93. I think you should state explicitly what criteria was used to define when individuals were apart from the main aggregation (for example, were these individuals more than a certain number of body lengths away from any other individual in the group)?*

Reply: We clarified the definition of omitted individuals (P3L96–L99, Fig. S3). In short, we excluded two fish that were more than twice the average-body-length from the main aggregation and that had no other fish in the direction in which they were heading or at their sides. We now indicate these two omitted individuals in Fig. S3.

Comment 7: *Line 95. Replace "... this heading direction vector..." with "... the length of the heading direction vector..." or "... the magnitude of the heading direction vector...".*

Reply: Done (P3L101).

Comment 8: *Line 97. Replace "... center of these two lines..." with "... intersection of these two lines...".*

Reply: Done (P3L103).

Comment 9: *Lines 102-105. I think some more explicit details about this process, and some re-wording, are needed. In particular, did you extrapolate the position of one fish at a time, and determine if it moved towards or away from its groupmates based on their static positions in the fossil? Or did you move all individuals at the same time, and compare all extrapolated positions post move (or something else)? Also, it might be best to re-iterate that the comparisons are made between nearest neighbours (rather than just "neighbouring individuals") on line 104.*

Reply: We have clarified that we moved all individuals at the same time, and then compared all positions at the next moment (P4L115–L117). Also, by "neighboring individuals" we actually meant "nearest neighbors". We have changed "neighboring individuals" to "nearest neighbors" in the revised manuscript (P4L116).

Comment 10: *Lines 116-117. The reference to "(also see main text)" is in the main text!*

Reply: Thank you for pointing out this. We have erased this phrase (P4L128).

Simulations

Comment 11: *Line 135. Why did you choose to do the simulations in a periodic domain (in both spatial dimensions) rather than an unbounded domain? In extreme cases, such as a group becoming very elongated in one spatial dimension, individuals at the front of the group may end up interacting directly with individuals at the rear of the group (and vice versa) due to the doubly periodic domain.*

Reply: We have clarified that we chose periodic boundary conditions to simplify calculations and not to separate the group (P4L149). We also explain that we used a large enough space to make sure that individuals at the front and end of a group do not interact with each other (P4L150–L151).

Comment 12: *Lines 137-138. The second behavioural rule has two separate additive components, an orientation term and an attraction term (as noted in the equation on line 145). In previous work (such as Couzin et al. (2002)), orientation and attraction effects have operated over separate zones, and* *have been treated as potentially different rules, before being combined in the same form of equation that you state on line 145. This leaves me unsure whether interactions within your second larger zone should be noted as a single rule, or a combination of rules (even though the overall effect is summarised by a single equation). At other points in the text (for example, on line 147), the zone where* $r_z < r < r_a$ *is referred to as an attraction zone, whereas it is explicitly a zone of both alignment/orientation and attraction; please take care not to refer to this model zone as just a zone of attraction throughout the text, because that may not be entirely accurate. Also, your analysis of potential movements in the group does seem to suggest the presence of repulsion and attraction effects, but nothing explicit about alignment (with theory suggesting alignment across a group can occur with or without an explicit alignment rule); why did you choose to include an explicit alignment term/rule in your model?*

Reply: As suggested, we now explain why we included an alignment term in our model (P5L154–161) and we rephrase "attraction zone" as "attraction-and-alignment zone" throughout the manuscript (P4L152; P5L168; P8L286). As the reviewer pointed out, we found both attraction and repulsion but no evidence of alignment behaviors from the fossilized shoal. This is because we could not find a way to test if there is a trace of alignment behavior from one snapshot of the collective movement, or small sample size. However, as the reviewer also pointed out in other comments, most extant fish species align via direct alignment behaviors or rather by combining attraction and repulsion behaviors, suggesting that it is reasonable to assume that *E. levatus* also has some alignment mechanism. In the zone model, specifying an alignment behavior for a particular zone is the most effective mechanism. Thus, we included the alignment term, additive to the attraction rule, as in a previous study (Hensor et al. 2005, Modelling density-dependent fish shoal distributions in the laboratory and field, Oikos).

Comment 13: *Lines 133-157. What rules did the model fish use to adjust their speed (if any)? You note on lines 152-153 that "Once its direction was determined, the fish moved with a speed of* $|v_i(t + \Delta t)|$*, which was limited to a range given in Table S1.", but this sentence effectively just says that the speed of the fish was its speed. Were changes in speed governed by particular rules or equations, or chosen randomly over the given range of 3-7 units, or something else (please provide details)?*

Reply: Thank you for this comment. The expression you quote was mistyped and should have read $|d_i(t + \Delta t)|$, the value of which can vary. Thus, we made the length of the speed vector $|vi(t)| = |d_i(t + \Delta t)|$ within a range of 3–7, which is truncated outside of this range (P5L173–175).

Comment 14: *Table S1. (In the SI.) What lead you to use these particular parameter values?*

Reply: We have clarified that we chose these parameter values arbitrarily within the ranges used in the previous study (Couzin et al. 2002, Collective memory and spatial sorting in animal groups, Journal of Theoretical Biology) because the purpose of our simulation is to test if the inferred potential behavioral rules are capable of recreating the similar patterns observed in the fossilized fish shoal

(P5L178–181; See also the Reply to the Comment 21).

Results and Discussion

Comment 15: *Lines 165-166. I think that references to papers 16-18 here might not be quite correct. Fig 5a. of reference 16 shows distributions of first, second and third nearest neighbours as a function of the distance to these neighbours, but not the sort of detail about laterally positioned neighbours that is shown in your overhead frequency distribution plot for nearest neighbours in your Fig. 1C. Neither Herbert-Read et al. (2011) nor Calovi et al. (2017) present graphs of relative frequency as a function of relative neighbour coordinates or distances. As a point of reference, the following papers present plots similar to your larger plot in Fig. 1C for a variety of species (although some of these plots are constructed based on the relative positions of all neighbours, not just nearest neighbours, as noted):*
Lukeman et al. (2010) Inferring individual rules from collective behavior, PNAS 107(28):12576-12580 (Fig 2. A for surf scoters, plot generated using all neighbours, with greatest frequencies occurring in front and behind the focal individual).
Katz et al. (2011) (as already in your reference list, Fig. 1B for pairs of golden shiners, again with greatest frequencies occurring in front and behind the focal individual).
Schaerf et al. (2017) The effects of external cues on individual and collective behavior of shoaling fish, Science Advances 3:e1603201 (Fig. 6 for x-ray tetras, plot generated using all neighbours, with greatest frequencies occurring to the sides of the focal individual, as is the case with your nearest neighbour plot).
Ward et al. (2017) Local interactions and global properties of wild, free-ranging stickleback shoals, Royal Society Open Science 4:170043 (Fig. 5 (a) for three-spine sticklebacks, plot generated using all neighbours for wild groups of at least 10 fish, with greatest frequencies occurring to the sides of the focal individual).
Raven et al. (2017) The role of biotic and abiotic cues in stimulating aggregation by larval cane toads (Rhinella marina), Ethology 123:724-735 (Figure 2 for cane toad tadpole aggregations, with greatest frequencies occurring to the sides of the focal individual).
Herbert-Read et al. (2017) Anthropogenic noise pollution from pile-driving disrupts the structure and dynamics of fish shoals, Proceedings of the Royal Society B 284:20171627 (Fig. 1 (b) for juvenile seabass, plot generated using nearest neighbours, with greatest frequencies occurring to the sides of the focal individual (equivalent to your results)).

Reply: Thank you very much for this helpful comment. We checked these articles and replaced some of our references based on your suggestion (P5L194–P6L196).

Comment 16: *Lines 179-180. I think you need to be careful with your wording here, the way the sentence is written makes it seem like it's been established that the main rules of interaction for all extant fish are repulsion and attraction-like rules. Based on published analysis, it does seem that golden shiners and eastern mosquitofish make primarily repulsion and attraction based adjustments* *to their velocity (Katz et al. 2011 and Herbert-Read et al. 2011), but explicit analysis of another species (guppies) suggested that there may also be a tendency to align with other group members (see Fig. 5 (b) and associated discussion in Herbert-Read et al. (2017) How predation shapes the social interactions of shoaling fish, Proc R Soc B 284:20171126). There is also evidence that there may be a tendency to align in groups of xray tetras (Fig 7. in Schaerf et al. (2017) The effects of external cues on individual and collective behavior of shoaling fish, Science Advances 3:e1603201) and three-spine sticklebacks (Fig 5. (b) in Ward et al. (2017) Local interactions and global properties of wild, free-ranging stickleback shoals, Royal Society Open Science 4:170043), but neither of these studies perform the explicit analysis used by Katz et al. 2011, Herbert-Read et al. 2011 or Herbert-Read et al. 2017 to further explore if there really is an alignment interaction occurring or not.*

Reply: We rephrased the sentence not to say that attraction and repulsion rules are general in all extant species but to clarify that some extant fish species use this rule in coordinated collective motion (P6L211–L212).

Comment 17: *Line 184. Maybe it would be better to write "tend to attack" rather than "are* supposed *to attack"?*

Reply: We have rewritten the phrase as suggested (P6L216).

Comment 18: *Lines 186-187. The polarisation is not "the absolute value of the mean individual heading direction", and the stated formula is also incorrect. One way determine the polarisation is to construct unit vectors in the facing directions of each of your fish, which could be denoted v_i as you have used. Then, to determine the polarisation: add all the individual unit vectors, determine the magnitude/length of the resultant vector (from the sum of individual unit vectors), and then divide the length of the resultant vector by the number of group members, N. Using your notation, the formula for the polarisation could then be written as:*

$\rho = \frac{1}{N}\left|\sum_{i=1}^{N} v_i\right|$ *(the error in your formula was just a minus sign in front of the sum).*

Reply: According to the comment, we have corrected the formula for the polarization parameter (P6L218–L220), which does not change the results of calculation.

Comment 19: *Lines 190-191 and 216-217. Perhaps it is not necessary to remove the individuals with the almost opposite headings to that of the bulk of the group from your analysis? A polarization of 0.902 is already quite high for a dynamic fish shoal, and it seems plausible to me that the orientations of the fish may not have been modified.*

Reply: As suggested, we have omitted the analysis in which individuals with aberrant headings were dropped (P6L222, Fig. 3C).

Comment 20: *Line 221. The referencing style for ref 23 does not seem consistent.*

Reply: We have corrected this (P7L256).

Comment 21: *Lines 235-250. This is the part of the study that I found least convincing, and perhaps the connection between the empirical and simulation analysis could be strengthened. First, I think that your choices of using a set of 1000 simulations, and using data from the 10000th time step (when transient behaviour in the model has likely disappeared) to compare with your data are completely reasonable. I also think that your comparison of the length to width ratio of the fossil and simulated groups is reasonable. What I'm not sure about is your choice to include an explicit alignment/orientation rule in your model, when your data analysis picks out just repulsion and attraction effects. It might be better (or more convincing at least?) to start out with a model that only has explicit repulsion and attraction effects. As I noted earlier, one such model is that described by (D'Orsogna et al. (2006) Self-propelled particles with soft-core interactions: patterns, stability and collapse, Physical Review Letters 96:104302), with another helpful description of the model in (Cañizo et al. (2010) Collective behavior of animals: swarming and complex patterns, Arbor 186:1035-1049). The model is a differential equation model, and the ranges over which repulsion and attraction effects work are not as easy to interpret as in the zonal model of Couzin et al. (2002) (just by looking at the equations), but it is possible for parallel motion to emerge from just repulsion and attraction in the model (which seems better aligned with your empirical work). If you did choose to explore what happens with the D'Orsogna model, then (using the notation and model formulation from Cañizo et al. (2010)) one set of parameters that can lead to parallel group motion (after about 5000 time steps) is $\alpha = 1$, $\beta = 1$, $C_A = 100$, $C_R = 50$, $l_A = 50$, $l_R = 5$ with a particle speed of 5 units per unit time. I'd also suggest using an explicit scheme for doing the time-stepping/time-integration for the system (like Euler's method, or a second or fourth order Runge-Kutta method with time steps, $\Delta t = 0.1$), as opposed to an implicit method or package solver (otherwise the calculations will take a huge amount of time). I also think that you need to explain somewhere in your text why you chose the particular model parameter values that you used (as per my comment in the simulations section). It might be worthwhile for you to look at the approach that Lukeman et al. (2010) used to try toa match model output with empirical results as well; this includes a systematic approach to identifying what types of interactions should be included (or not).*

Reply: Thank you for this suggestion. Following the comment, we analyzed the differential equation model shown in D'Orsogna et al. (2006) and Cañizo et al. (2010) with the suggested parameter values (i.e., $\alpha = 1$, $\beta = 1$, $C_A = 100$, $C_R = 50$, $l_A = 50$, $l_R = 5$). We used the Runge-Kutta method with time steps, $\Delta t = 0.1$. However, this model produced patterns with much higher polarization ($\rho > 0.99$), but without an oblong shape (length-width ratio of the bounding box ≈ 0.9) or as clear a trace of interaction rules as in our individual-based model simulations. Moreover, in the revised manuscript, we now clarify why we used the model with the alignment rule (P5L154–L161; see also the Reply to the Comment 12). Thus, we did not include the results of this differential equation model. Also, we clearly explained that we chose our parameter values arbitrarily within the similar ranges used in the previous study (Couzin et al. 2002, Collective memory and spatial sorting in animal groups, Journal of Theoretical Biology) (P5L178–183; See also the Reply to the Comment 14). This is because the purpose of our simulation is to test if the inferred potential behavioral rules are capable of recreating patterns similar to that observed in the fossilized fish shoal. As the information we can obtain from the fossil is limited (because of snapshot and thus small sample size), we did not try to estimate parameter values from the fossilized shoal. For example, it is nearly impossible to measure the moving speeds or perceptional ranges of individuals.

Comment 22: *Lines 246-247, and Fig 3. D. One of the key features from your equivalent plot for the fossil data was the more frequent appearance of nearest neighbours to the sides of an individual (compared to the front and back). However, your simulation results show greater frequencies of nearest neighbours to the front and back of individuals as compared to the sides, which might suggest that your model might not be quite right in detail (perhaps due to parameter choices within your model, or the form of the model). I think that if you were able to adjust your model to give results consistent with greater frequencies of nearest neighbours in lateral positions it would make the connection between model and simulation more convincing. (I know it may be hard to do this though, so if you cannot generate the same structure in relative positions of nearest neighbours with your model, you could still discuss the differences between simulated and empirical data and what the difficulties might be in getting a simulation to match reality in this case.)*

Reply: In the revised manuscript, we have clarified that we could not recreate the same structure in relative positions of nearest neighbors with our simulations within the range we explored (P8L298–303). This may be because actual fish have body shapes that are elongated along the direction of motion (see also the Reply to the Comment 5), while the agents in our simulations are simply points without physical bodies. The *SI* text of Ballerini et al. 2008 similarly notes that the numerical models fail to reproduce the observed structural anisotropy, probably for the same reason.

Comment 23: *Also, note that "Distance" is spelt incorrectly on the vertical and horizontal axis labels on Fig. 3.*

Reply: Thank you for this comment. We have corrected Fig. 3.

Comment 24: *Lines 269-270 and 272-273. These statements leapt out at me as being a bit too strong. I think you need more evidence to convince a reader that the fish were shoaling solely to avoid predators (although this is a reasonable possibility), and that the predation pressure was high (rather than just an existing pressure).*

Reply: According to the comment, we rephrased the sentences to weaken these claims (P9L322–323; P9L324–326).

Comment 25: *Lines 281-285. Repulsion and attraction rules also seem to appear in the behaviour of guppies (another species in the Cyprinodontiformes order, analysis in Herbert-Read et al. (2017) How predation shapes the social interactions of shoaling fish, Proc R Soc B 284:20171126), and xray tetras (from the Characiformes order, analysis in Schaerf et al. (2017) The effects of external cues on individual and collective behavior of shoaling fish, Science Advances 3:e1603201). It might bolster your discussion to include these, as you then have five species across three different orders exhibiting repulsion and attraction consistent behaviour, in addition to E. levatus. It is also very interesting that the repulsion/attraction type rules of interaction are consistent across these species (even if the details of how repulsion and attraction work m*ight *differ between species).*

Reply: Thank you for this helpful comment. We have added information on these species to the references (P10L335–L339; P10L340–341).

Appendix C

Response to Referees

Referee1:

As previously, I think this is a fascinating paper and am satisfied with the changes undertaken by the authors. Doubts remain, but these are acknowledged. Looking forward to seeing it in print.

Reply: Thank you so much.

Referee2:

I think that the authors have done a good job addressing both my comments and referee 1's comments in their revised manuscript, and suggest that this very interesting and novel article should be published. In working through the revised manuscript, I had the following thoughts that the authors might consider if they have the opportunity to make any more small revisions to the article (see the attached pdf).

Reply: Thank you for these comments. We revised the manuscript accordingly.

Simulations

Comment 1: *Lines 149-150: I'm not sure that it's a convincing argument that the periodic boundary conditions simplify calculations. From experience, such conditions make implementing a self-propelled particle model more complex than in the case of an unbounded domain, as any calculations that involve determining the distance between individuals have to take into account the periodicity of the domain in x and y. On the other hand, the periodicity does mean that group members essentially have a maximum distance to other group members enforced, so the argument about avoiding separation of the group is reasonable.*

Reply: Thank you for this comment. We removed the part to just mention that we chose periodic boundary conditions to avoid separation of the group (P4L149).

Comment 2: *Lines 161-162: It might help avoid some ambiguity by writing "If there were other fish j within a distance r_z of fish i, then fish i avoided these fish by turning towards direction: ..."*

Reply: We changed as suggested (P5L162).

Results and Discussion

Comment 3: *Lines 218-219: Perhaps "This parameter is calculated by dividing the length of the sum of individual unit vectors in the direction of motion of each individual, $\hat{v}_i$, by the number of group members. That is, $\rho = \frac{1}{N}|\sum_i^n v_i|$, where N is the number of group members."? Just so there is some* *distinction between the velocity vectors that appear in the model, and direction only vectors used to determine the group polarisation.*

Reply: Thank you for indicating a confusing point. Actually, velocity vectors in the model and unit vector used to calculate group polarization are different. To avoid confusion, we used u instead of v for unit vectors to calculate group polarization in the revised manuscript (P6L218-220).

Supplementary Information

Comment 4: *Fig S4 caption, last sentence. Given that you've changed the description in the main text, for consistency you could write "The position of the fish was determined as the point of intersection of these two lines (red point)".*

Reply: Done (*SI*).

Responses to Referees – Referee2

Comment 5: *Reply to comment 21: Given that you've gone through the effort of trying out the calculations that I suggested, it might be worth reporting that you did these calculations (in the supplementary information at least), and that you weren't able to generate elongated groups like those seen in the fossil, or your other simulations, when applying a model based solely on repulsion and attraction effects (at least for the parameters that you examined). I think this adds a bit more weight to why you have an alignment effect in your chosen model as well, and perhaps adds further to speculation that E. levatus could have had some instinctual movement rule based around alignment with other group members.*

Reply: We added the discussion about the model only with repulsion and attraction rules in the supporting information (*SI*).