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Local interactions and their group-level consequences in flocking jackdaws

Hangjian Ling, Guillam E. McIvor, Kasper van der Vaart, Richard T. Vaughan, Alex Thornton and Nicholas T. Ouellette

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Review timeline

Original submission:	28 February 2019
1st revised submission:	11 April 2019
2nd revised submission:	24 May 2019
Final acceptance:	7 June 2019

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

Review History

RSPB-2019-0505.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?
Excellent

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?
N/A

Is it clear?
N/A

Is it adequate?
N/A

Do you have any ethical concerns with this paper?
No

Comments to the Author
The manuscript describes how collision avoidance in flocks of jack daws happens by turning rather than by changing speed and how this may lead to a wide group shape. The paper is fine, I just have comments on placement of references and some issues with wording and specification.

Line 47 argues that bird flock are modelled with agent based models, here readers will like to see models specific to bird flocks such as those by Hemelrijk and Hildenbrandt, please add here. The reference to Hogan and co-authors (Hogan et al. 2017) is misplaced here because it concerns the reaction of human predators to flocks.
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references
Hemelrijk CK, Hildenbrandt H (2012) Schools of fish and flocks of birds: Their shape and internal structure by self-organization. Interface Focus 2:726–737. doi: 10.1098/rsfs.2012.0025
Hogan BG, Hildenbrandt H, Scott-Samuel NE, et al (2017) The confusion effect when attacking

simulated three-dimensional starling flocks. R Soc Open Sci 4:. doi: 10.1098/rsos.160564

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?
Good

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

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

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.
Yes

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?
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Comments to the Author
Dear authors,
I found this an interesting paper and am happy to see new data arriving in the flocking literature, along with an attempt to begin some hypothesis comparison, or at least comparison of models to results. However, I found the analysis incompletely described and am not sure at this point whether some of the conclusions described are particularly well supported by your data.

In an attempt to better understand your results I downloaded the data files from FigShare and spent some time attempting to recreate parts of Figure 4. This was not particularly successful, but did raise some questions about your analysis workflow that should be described in your Methods or, if necessary, in the supplement. First, the figure caption says that the data were "averaged over 305 pairs", but the sampling density of average neighbor locations does not seem to support the sort of spatial histograms shown here in 4B & C, so it appears that the continuous data from each pair was used and then averaged by spatial location? Second, my recreation attempt suggests that you calculate repulsion force F twice for each pair, enforcing symmetry in the spatial histograms and making the distinction between positive and negative portions of each axis meaningless; if you're going to do this all data should be reflected into one quadrant. Also, I found very large variances when I attempted to reproduce Figure 4D. This suggests that the "error bars smaller than symbol size" are the result of computing a standard error with a large sample size, but I couldn't find a description of the sample size, which in any case shouldn't be larger than the number of pairs that contributed to that data point. I also don't understand the magnitude of the color scale in the spatial histograms 4B & C; the color bar scale has a limit of only 0.5 m/s^2, but 0.5 is much less than the overall mean magnitude of the F I calculated, and similar to the mean of means magnitude so I'm further confused on exactly how your data were processed to produce the results shown. I was also unable to reproduce the flapping frequency results from Fig. 7b & c, though it isn't clear which dataset these were drawn from. Overall, the documentation of how the results shown in this paper were arrived at seems quite lacking. I suggest you take the time to fully document your procedures in the Methods and supplement and/or add your processing code to FigShare.

Other notes:
The title should be "Local interactions and their group-level consequences in Jackdaws", there is insufficient generality in this study to claim it covers "flocking birds" as a type

Line 87 – Has anyone hypothesized aerodynamic interactions in this sort of side by side flock? Why should a bird match flapping phase with another bird offset laterally that is not creating a wake or flow field that the focal bird could interact with? Also, inspection of the Portugal et al paper shows that although there is a tendency toward phase matching, it is far from a universal occurrence even in birds believed to be taking aerodynamic advantage of a wake so it is unclear what frequency matching threshold should be applied to support or refute an aerodynamic interaction.

Line 116 – what is the body size of a Jackdaw?

Line 192 – Please discuss these position relationships quantitatively in units relevant to the birds, e.g. the number of body lengths or wing spans.

Line 197 – If birds avoid collisions mainly by turning then presumably there is a high-magnitude Fwing zone ahead of the focal bird, can this be demonstrated?

Line 199 – shouldn't the average a be close to zero regardless? Maybe look at |a| or the variance?

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Line 224 – I'm not entirely clear on what you're claiming to show here. Is it that the weaker travel direction forces lead to the group splitting into subgroups along the travel direction, that the subgroups have a larger wing direction extend due to the stronger wind direction forces, or both?

Line 227 – Shouldn't this analysis be restricted to birds flying in a position where they might interact aerodynamically, rather than the simple nearest neighbor for all birds? See also comments to Line 87.

Line 240 – Do you know that the positive speeding force for an ahead neighbor is due to the focal bird speeding up or the neighbor slowing down? Similarly, do you know which bird is changing its flapping frequency away from default?

Line 241 – Lateral maneuvers in birds can also be powered by loss of kinetic or potential energy rather than flapping, e.g. by turning with wings extended so as to minimize wing loading during the maneuver and increasing flapping frequency later to regain that energy. An accounting of whether lateral maneuvers are in fact cheaper needs to consider more than just flapping frequency – please expand this analysis to cover other possible costs.

Line 284 – The discussion in the results was on how subgroups are elongated in the wing direction; is this also true of the whole group? Inspection of figure S2 seems to show a variety of whole-group bounding box aspect ratios.

Line 298 – The physics of bird flight are strongly affected by flight speed; are the social forces similarly affected? The speed range in the pairwise data suggests that you should have enough of a speed range to investigate this and better knit together bird flocking and bird flight physics.

Table 1 – The Isolated pairs number of birds is 610 or 710?

Decision letter (RSPB-2019-0505.R0)

01-Apr-2019

Dear Dr Ling:

I am writing to inform you that your manuscript RSPB-2019-0505 entitled "Local interactions and their group-level consequences in flocking birds" 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.
2) A clean copy of the manuscript and one with 'tracked changes' indicating your 'response to referees' comments document.
3) Line numbers in your main document.

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Sincerely,

Proceedings B
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
As you will see, both reviewers find your manuscript interesting, but Reviewer 2 raises some serious concerns regarding the description of the methods, the statistical analysis of the data, and its presentation in Fig. 4. These points would all need to be addressed through a Major Revision before we could consider your manuscript further for possible publication in Proc. B. Please attend to all of the points raised by the reviewers. Since this manuscript presents a new analysis of published data, please ensure that your revision and response clarifies the novelty of the current manuscript and its relationship to your earlier paper in J. R. Soc. Interface and any other related work on this dataset.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
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Table 1 – The Isolated pairs number of birds is 610 or 710?

Author's Response to Decision Letter for (RSPB-2019-0505.R0)

See Appendix A.

RSPB-2019-0865.R0

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?
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.
Yes

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
See attached MS Word file. See Appendix B

Decision letter (RSPB-2019-0865.R0)

10-May-2019

Dear Dr Ling:

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.

When revising your manuscript you should also ensure that it adheres to our editorial policies (https://royalsociety.org/journals/ethics-policies/). You should pay particular attention to the following:

Research ethics:
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.

Use of animals and field studies:
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. 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,

Proceedings B
mailto: proceedingsb@royalsociety.org

Associate Editor Board Member
Comments to Author:
Thank you for revising your manuscript in response to the Reviewers' comments. You will see that whilst the Reviewer finds your revised manuscript to be of interest, they have also raised some detailed and very helpful comments in light of the information provided that will need to be addressed before we can make a final decision. Please attend to all of these comments in preparing your revision.

Reviewer(s)' Comments to Author:

Referee: 2

Comments to the Author(s).
See attached MS Word file.

Author's Response to Decision Letter for (RSPB-2019-0865.R0)

See Appendix C.

Decision letter (RSPB-2019-0865.R1)

07-Jun-2019

Dear Dr Ling

I am pleased to inform you that your manuscript entitled "Local interactions and their group-level consequences in flocking jackdaws" 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.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

If you have any queries regarding the production of your final article or the publication date please contact procb_proofs@royalsociety.org

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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,

Dr Sasha Dall
Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Associate Editor:
Board Member
Comments to Author:
Thank you again for submitting your interesting work to Proc. B, and for the care taken in addressing the comments of the reviewer.

Appendix A

Response to Referee 1

The manuscript describes how collision avoidance in flocks of jackdaws happens by turning rather than by changing speed and how this may lead to a wide group shape. The paper is fine, I just have comments on placement of references and some issues with wording and specification.

Response: We thank the reviewer for the positive feedback and the constructive comments.

Line 47 argues that bird flock are modelled with agent based models, here readers will like to see models specific to bird flocks such as those by Hemelrijk and Hildenbrandt, please add here. The reference to Hogan and co-authors (Hogan et al. 2017) is misplaced here because it concerns the reaction of human predators to flocks.

Response: We thank the reviewer for the suggestion. The reference by Hogan *et al.* (2017) has been moved to line 58. The reference by Hemelrijk and Hildenbrandt (2012) has been added here.

Line 55 Here still bird flocks are under concern, so it is better to cite Hemelrijk and Hildenbrandt 2012 than their work on fish schools.

Response: We agree. In this line, the reference by Hemelrijk *et al.* (2010) has been replaced by the Hemelrijk and Hildenbrandt (2012).

Line 57 perhaps add here the reference to Hogan and co-authors (presently reference number 40).

Response: We agree. The reference to Hogan *et al.* (2017) has been added here.

Line 63-66 Can you make the connection between forces in the work by Lukeman and acceleration explicit?

Response: In the work by Lukeman *et al.* (2010), they fit observational data to a zonal model where individuals' accelerations are determined by a combination of attraction/alignment/repulsion forces, autonomous self-propulsion forces, and a noise term (so that $mdv/dt = F_{\text{interaction}} + F_{\text{self-propulsion}} + \text{noise}$). This zonal model was described in details in by Levine *et al.* (2001). To reflect these points, the sentences in lines 64 to 67 have been modified, and a new reference that describes the zonal model used by Lukeman *et al.* (2010) has been cited.

Line 81, turning based repulsion leading to side-by side structure, perhaps refer to work on bearing angle by (Hemelrijk and Hildenbrandt 2012)

Response: The reference to Hemelrijk and Hildenbrandt (2012) has been added here.

Lines 196-200 about concluding that avoidance of collisions happens by turning. I do not see where it is shown. In the figures it is not clear what -0.2 and -0.5 mean in table 1 and fig 4d and 5.

Response: In lines 187 to 194, we explain that a short-range repulsion zone is only observed in the map of the turning force (Figure 4b), not in the map of the speeding force (Figure 4c). It is based on this evidence that we conclude that "collision avoidance is mainly achieved by turning". To reflect this point, the sentence in line 194 was modified to: "...The observation that repulsion is only present in the map of the turning force indicates that birds avoid collisions mainly by turning... ”

The values on the y-axis of Figures 4d and 5 are the acceleration of a focal bird relative to its neighbour, as we explain in the Methods section (so that $F=a^{focal}-a^{neighbour}$). In lines 176 to 178, we explain “...positive (negative) F_{Speed} implies speeding up (slowing down), and positive (negative) F_{Turn} implies turning right (left)...” In the caption of Table 1, we explain: “...Positive (negative) values of a_{Move} mean speeding up (slowing down), and positive (negative) a_{Wing} implies turning right (left)...”

Line 199,200: where is shown that a_wing is larger a_movement? Unclear whether this refers to absolute values perhaps.

Response: Our apologies; we intended to say that the standard deviation of a_{wing} is larger the standard deviation of a_{move}. We have corrected the sentence in line 197 to read: “...The anisotropy of the force in the wing and movement directions is consistent with the observation that the standard deviation of ***a*** in the wing direction was larger than that in the movement direction (Table 1)...”

Line 203: ‘stronger’ it seems also weaker, perhaps authors want to say ‘more extreme’?

Response: By saying ‘stronger’, we mean the absolute value of the force is larger. We have clarified the wording in line 203: “...with the absolute value of the turning forces larger than that of the speeding forces...”

Line 219: subgroups in terms of what? Speed or acceleration?

Response: The subgroups are separated based on bird position. Typically, the distribution of bird position along the flight direction shows multiple peaks (Figure 6(d) and *electronic supplementary material figure S5*). We determined the number of subgroups based on the number of peaks. More details on this can be found in the response to Referee 2 below.

Response to Referee: 2

I found this an interesting paper and am happy to see new data arriving in the flocking literature, along with an attempt to begin some hypothesis comparison, or at least comparison of models to results. However, I found the analysis incompletely described and am not sure at this point whether some of the conclusions described are particularly well supported by your data.

Response: We thank the reviewer for the positive feedback and helpful comments. Below is a point by point response to each comment.

In an attempt to better understand your results I downloaded the data files from FigShare and spent some time attempting to recreate parts of Figure 4. This was not particularly successful, but did raise some questions about your analysis workflow that should be described in your Methods or, if necessary, in the supplement. First, the figure caption says that the data were “averaged over 305 pairs”, but the sampling density of average neighbor locations does not seem to support the sort of spatial histograms shown here in 4B & C, so it appears that the continuous data from each pair was used and then averaged by spatial location?

Response: We are very pleased that the reviewer was interested enough to test our data uploaded to FigShare, and very much appreciate the reviewer's feedback for making the description of our methods more precise. Our analysis was indeed based on the continuous data, not on one sample from each pair. Each pair provided an average 490 samples. We used a total of 149,230 samples from the 305 pairs to obtain the results presented in Figure 4. To reflect those points, we made the following changes:

- The potentially misleading sentence in the caption of Figure 4: "...Data in (b-d) are obtained by averaging over 305 isolated pairs..." was modified to: "...Data in (b-d) were obtained from 149,230 samples taken from 305 isolated pairs (*see electronic supplementary material*)..."
- We added a new section in the *electronic supplementary material* named: "*Calculation of two-dimensional force maps and one-dimensional force curves*". In this new section, we give a full description of our data analysis procedure.
- We have uploaded our data analysis code (written in Matlab) to FigShare along with the data at https://figshare.com/s/490054bef08b27604934. We have also uploaded our data in a format that can be read directly by Matlab. In each code, we provide a detailed description of how to load and use the data, the data format, and the workflow. And, as an example, we added a section in *electronic supplementary material* named: "*Sample data analysis code*". In this section, we give a step-by-step description of the data analysis code used to generate of Figure 4.
- In the main text, we refer to the new sections in line 181: "...The details of our calculation of two-dimensional force maps and one-dimensional force curves are described in the *electronic supplementary material*..."
- The phrase in line 152: "...providing a total 74,615 data points..." was deleted.

Second, my recreation attempt suggests that you calculate repulsion force F twice for each pair, enforcing symmetry in the spatial histograms and making the distinction between positive and negative portions of each axis meaningless; if you're going to do this all data should be reflected into one quadrant.

Response: The reviewer is right. We calculated the force twice for each pair, since either bird can be treated as the focal one. By doing this, it is true that the force map is forced to be antisymmetric with respect to d_{Wing} and d_{Move}. However, we would prefer to present the data in the present form, instead of just one quadrant, for two reasons: (i) since the neighbour bird can be found either in front or behind, showing the full force map reflects the force distribution for all possible neighbour locations; and (ii) showing the full map makes it easier make qualitative comparisons with results reported from fish schools (e.g., Katz *et al.*, 2011).

To reflect these points, in the new section of the *electronic supplementary material* "*Calculation of two-dimensional force maps and one-dimensional force curves*", we describe how we selected the focal birds for the calculation of F and the reasons why we presented the full force maps and curves (i.e., for both positive and negative values of d_{wing} and d_{move}).

Also, I found very large variances when I attempted to reproduce Figure 4D. This suggests that the "error bars smaller than symbol size" are the result of computing a standard error with a large sample size, but I couldn't find a description of the sample size, which in any case shouldn't be larger than the number of pairs that contributed to that data point.

Response: We thank the reviewer for pointing this out. The error bars in the figure caption are standard errors. Since we had a total 149,230 samples from the 305 isolated pairs, the standard errors were very small due to the large sample size. The sentence in the caption of Figure 4: "...Error bars are smaller than the symbol size..." was modified to: "...Each point in (d) was calculated by averaging 7,000 to 30,000 samples, and has a standard error smaller than the symbol size...”

I also don’t understand the magnitude of the color scale in the spatial histograms 4B & C; the color bar scale has a limit of only 0.5 m/s^2, but 0.5 is much less than the overall mean magnitude of the F I calculated, and similar to the mean of means magnitude so I’m further confused on exactly how your data were processed to produce the results shown.

Response: The mean values of F_{Speed} and F_{Turn} from all 149,230 samples are about -0.01 m/s^2 (Figure R1). Therefore, the magnitude of 0.5 m/s^2 shown in Figure 4 is in fact much larger than the overall mean magnitudes of F_{Speed} and F_{Turn}. The detailed data analysis procedure can be found in our uploaded Matlab codes and *electronic supplementary material*.

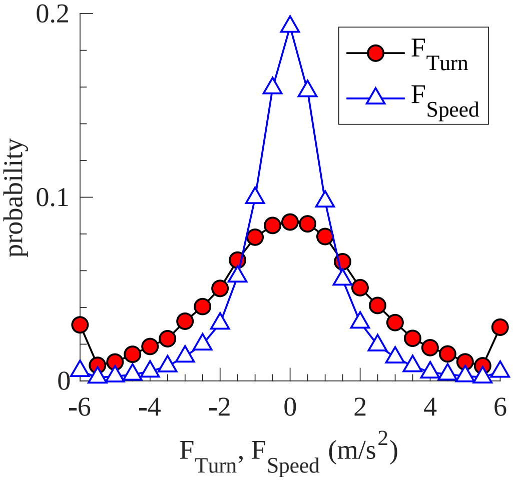


Figure R1. Probability density distributions of F_{Turn} and F_{Speed} of the 149,230 samples. The average values of F_{Turn} and F_{Speed} over the 149,230 samples are -0.01 m/s^2.

To reflect this point, we added a sentence in caption of Figure 4 that: “...0.5 m/s^2 is much larger than average values of F_{Turn} and F_{Speed} over the 149,230 samples... ”

I was also unable to reproduce the flapping frequency results from Fig. 7b & c, though it isn’t clear which dataset these were drawn from.

Response: The results in Figures 7b and c were calculated from the 149,230 samples from the isolated pairs. We add in the caption of Figure 7 that: “...Results were obtained from 149,230 samples taken from 305 isolated pairs...” The sample sizes for large groups are somewhat smaller due to shorter trajectories, and are not large enough to calculate reliable wingbeat frequency data. That is why we only presented data for isolated pairs.

Overall, the documentation of how the results shown in this paper were arrived at seems quite lacking. I suggest you take the time to fully document your procedures in the Methods and supplement and/or add your processing code to FigShare.

Response: Just as in mentioned above, we added new sections in the *electronic supplementary material* “*Calculation of two-dimensional force maps and one-dimensional force curves*” and “*Sample data analysis code*” to fully document the data analysis procedure. We have also added all the data processing code to FigShare. In the section on Data accessibility, we have added the sentence: “...We also provide the data processing codes for generating Figures 4 to 7... ”

Other notes:

The title should be “Local interactions and their group-level consequences in Jackdaws”, there is insufficient generality in this study to claim it covers “flocking birds” as a type.

Response: This is a fair comment. We have changed the title to: “Local interactions and their group-level consequences in flocking jackdaws”.

Line 87 – Has anyone hypothesized aerodynamic interactions in this sort of side by side flock? Why should a bird match flapping phase with another bird offset laterally that is not creating a wake or flow field that the focal bird could interact with? Also, inspection of the Portugal et al paper shows that although there is a tendency toward phase matching, it is far from a universal occurrence even in birds believed to be taking aerodynamic advantage of a wake so it is unclear what frequency matching threshold should be applied to support or refute an aerodynamic interaction.

Response: We agree with the reviewer: in a side-by-side flight configuration, since the neighbour birds are not located in the wake region, whether the flap phases match or not is not related to aerodynamic interactions. We are not aware of any papers studying the flow field and aerodynamic interactions in such a side-by-side configuration. Without measuring the detailed flow field, we agree that only showing a lack of phase matching in our current study is not sufficient to arrive at a general conclusion. We have therefore decided to delete the discussion of aerodynamic interactions and leave it for future numerical or experimental studies. In light of this, we made the following modifications:

- In the Introduction, we deleted the paragraph at line 86.
- In the Results section, we deleted the paragraph at line 232.
- In line 233, we added the definition of df_{wb}.
- Figures 7(b) and (c) were renamed as Figures 7(a) and (b) respectively.
- We deleted the original *electronic supplementary material figure S4*.
- In the Discussion section, we deleted the sentences in line 262.
- In the Discussion section, the sentences in lines 262 to 265 have been modified.

Line 116 – what is the body size of a Jackdaw?

Response: Jackdaws typically have a body length of 34 to 39 cm. We have provided this value in this line in the revised draft.

Line 192 – Please discuss these position relationships quantitatively in units relevant to the birds, e.g. the number of body lengths or wing spans.

Response: We have now given these relationships in units of the typical jackdaw body length:

- We added a sentence at line 191: “...F_{Turn} switches from repulsive to attractive at $|d_{Wing}|=0.9$ m (≈2.5 jackdaw body lengths) ...”
- In line 212, we modified the sentence to: “...in that the most probable location for a neighbouring bird was at $|d_{Wing}|=1.0$ m (≈2.8 jackdaw body lengths) and $d_{Move}=0$...”

Line 197 – If birds avoid collisions mainly by turning then presumably there is a high-magnitude Fwing zone ahead of the focal bird, can this be demonstrated?

Response: Our conclusion that birds avoid collision mainly by turning is based on the evidence that we only observe a repulsion zone in the force map of F_{Turn}, not in the force map of F_{Speed}. This result indicates that repulsive force is mainly generated by turning. According to Figure 4(b), F_{Turn} has a peak value directly on the side of the focal bird, but there is no peak value directly ahead of the focal bird. To clarify this point, we have now explained more explicitly how we arrived the conclusion that birds avoid collision mainly by turning in line 194 by saying that: "...The observation that repulsion is only present in the map of the turning force indicates that birds avoid collisions mainly by turning..."

Line 199 – shouldn't the average a be close to zero regardless? Maybe look at |a| or the variance?

Response: The reviewer is right: the average $\boldsymbol{a}$ is close to zero. We meant to say that the standard deviation of a_{wing} is larger compared to that of a_{Move} (3.5 v.s. 1.6 m/s^2). The words in line 197 were thus modified to: "...the standard deviation of $\boldsymbol{a}$ in the wing direction was larger than that in the movement direction (Table 1)..."

Line 220 – How was the number of groups determined for k-means?

Response: For all the flocks in our study, we qualitatively observed that birds are typically separated into multiple subgroups along the flight direction. We determined the number of subgroups based on the number of distinguishable peaks in the distribution of bird position along the flight direction. For example, for flock #1, the distribution of bird positions along the flight direction shows two distinguish peaks (Figure R2(b)), while the distribution in the direction perpendicular to flight direction show no obvious peaks (Figure R2(c)). We then used *k*-means clustering to separate the entire group into two subgroups (Figure R2(a)), given the two peaks in the position distribution. Similar trends are also observed for flocks #2 to 6, as shown in a new *electronic supplementary material figure S5*.

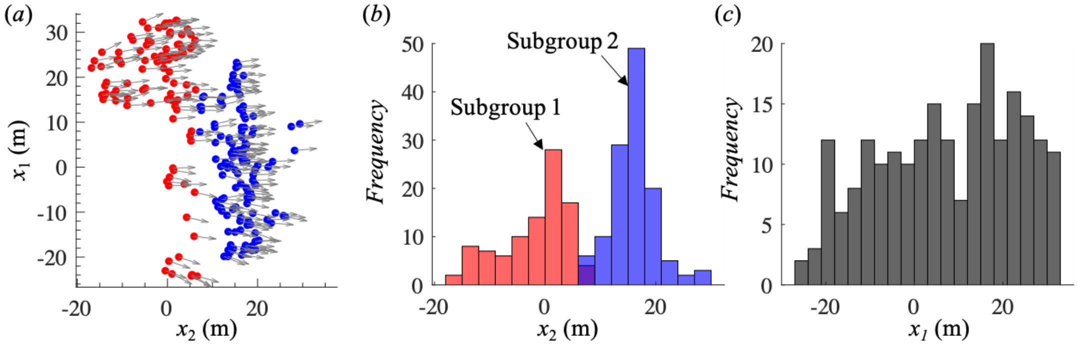


Figure R2. (a) Distribution of bird locations projected onto the horizontal plane. x_2 is aligned with the mean flight direction of all birds. The entire flock can be separated into two subgroups (one coloured in red, and the other in blue). The vectors indicate the movement directions of individual birds. (b-c) Probability of bird position along x_2 (b) and along x_1 (c) for birds shown in (a).

To reflect these points, we made the following modifications:

- Figure 6 was updated by adding Figure R2(a-b) showing the subgroups in flock #1.

- A new figure S5 showing subgroups for flocks #2 to 6 was added to the *electronic supplementary material.*
- In line 219, we refer to these new figures: *"...*As shown in figure 6(c) and *electronic supplementary material figure S5*, entire flocks typically appear to consist of several distinguishable subgroups separated along the movement direction...*"*
- In line 221, we described how the number of subgroups was determined.

Line 224 – I'm not entirely clear on what you're claiming to show here. Is it that the weaker travel direction forces lead to the group splitting into subgroups along the travel direction, that the subgroups have a larger wing direction extend due to the stronger wind direction forces, or both?

Response: This is a very helpful comment. Initially, we were unclear as to why the flocks are separated into subgroups along the movement direction. We agree with the reviewer that the weaker attractive force in the movement direction could be a reason for this observation. However, within each subgroup, the subgroup shape is elongated along the wing direction (Figure 6e), likely due to scaling up the side-by-side local neighbour structure, similar to the elongation of fish schools in the movement direction due to their front-to-back neighbour structure.

To clarify what point we are trying to make, we modified the sentence in line 225 to: "...We find that all subgroups are elongated in the wing direction (figure 6e), indicating that the side-by-side local structure does indeed percolate upscale and has group-level consequences. The generation of multiple subgroups along the movement direction is likely due to weaker attractive forces in that direction compared to the wing direction (Figure 5)..."

Line 227 – Shouldn't this analysis be restricted to birds flying in a position where they might interact aerodynamically, rather than the simple nearest neighbor for all birds? See also comments to Line 87.

Response: As with our response to the previous comment, we agree with the reviewer that aerodynamic interactions are only possible when a neighbouring bird is located in the wake region (and not on the side). We have therefore removed this paragraph in the revised paper.

Line 240 – Do you know that the positive speeding force for an ahead neighbor is due to the focal bird speeding up or the neighbor slowing down? Similarly, do you know which bird is changing its flapping frequency away from default?

Response: This is an interesting question. To answer it, we analyzed the 149,230 samples taken from 305 isolated pairs. First, we calculated the probability density functions (PDFs) of accelerations in the movement direction for rear birds and front birds (a_{Move}^{rear} and a_{Move}^{front}) for d_{Move}>1 m (in the positive speeding force region). As shown in Figure R3(a), both PDFs have negative and positive a_{Move} indicating that a positive speeding force can be caused by either the rear bird speeding up or the front bird slowing down. However, the rear birds have a slightly larger a_{Move} compared to the front birds ($\langle a_{Move}^{rear}\rangle - \langle a_{Move}^{front}\rangle = 0.26$ m/s^2), indicating that the rear birds are somewhat more likely to speed up than the front birds are to slow down. We also calculated the PDFs of wingbeat frequencies for rear birds and front birds (f_{wb}^{rear} and f_{wb}^{front}) for d_{Move}>1 m. As shown in Figure R3(b), the rear birds have slightly larger wingbeat frequencies compared to the front birds ($\langle f_{wb}^{rear}\rangle - \langle f_{wb}^{front}\rangle$=0.15 Hz), consistent with the slightly larger a_{Move} of the rear birds. Therefore, both the acceleration and wingbeat frequency imply that the rear birds are more likely to change their behaviour in response to the front birds.

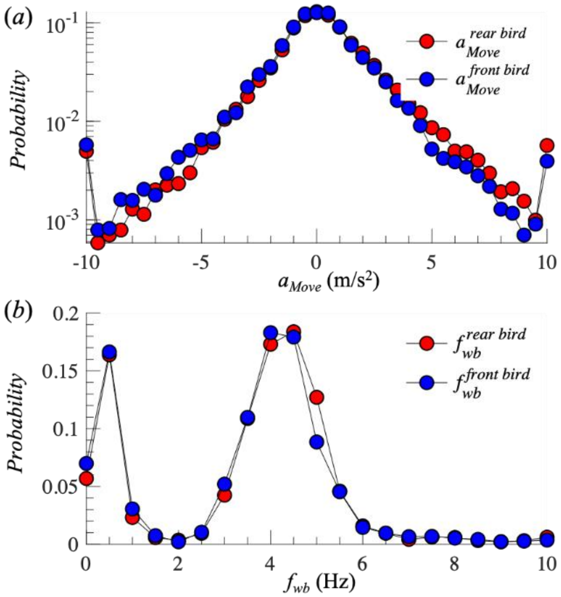


Figure R3. (a) Probability density functions of acceleration in the movement direction for rear and front birds in isolated pairs (a_{Move}^{rear} and a_{Move}^{front}). The average a_{Move}^{rear} is slightly larger than the average a_{Move}^{front} ($\langle a_{Move}^{rear}\rangle - \langle a_{Move}^{front}\rangle$ = 0.26 m/s^2). (b) Probability density functions of wingbeat frequency for rear and front birds (f_{wb}^{rear} and f_{wb}^{front}). The two peaks in each PDF of f_{wb} correspond to flapping and non-flapping flight. The average f_{wb}^{rear} is slightly larger than the average f_{wb}^{front} ($\langle f_{wb}^{rear}\rangle - \langle f_{wb}^{front}\rangle$ = 0.15 Hz). Data are obtained from the 149,230 samples taken from 305 isolated pairs.

To reflect these points, we added a new section in the electronic supplementary material named "*Comparison between front and rear birds in isolated pairs*". Figure R3 was added as electronic supplementary material figure S7. In the revised paper, we refer to this new section in line 241: "...Additionally, comparing between rear and front birds in isolated pairs shows that rear birds are more likely to change their behaviour (e.g., to generate positive speeding forces, rear birds are more likely to increase their wingbeat frequency and speed up) in response to front birds (see details in *electronic supplementary material*)... "

Line 241 – Lateral maneuvers in birds can also be powered by loss of kinetic or potential energy rather than flapping, e.g. by turning with wings extended so as to minimize wing loading during the maneuver and increasing flapping frequency later to regain that energy. An accounting of whether lateral maneuvers are in fact cheaper needs to consider more than just flapping frequency – please expand this analysis to cover other possible costs.

Response: This is a good point. We therefore examined the change of the total energy of a focal bird compared to that of the neighbour bird, denoted as $dE'=E'^{\text{focal}}-E'^{\text{neighbour}}$, where E' is the rate of change of the total energy ($E=0.5|\mathbf{v}|^2+gh$). E' is estimated as $E'=[E(t+dt)-E(t)]/dt$, where dt is the time step . Assuming a constant drag force, $E'>0$ indicates an increase of mechanical power output. Therefore, $dE'>0$ indicates that focal birds use more power than neighbouring birds. The dependence of dE' as a function of d_{Wing} and d_{Move} is shown in Figure R4 (c-d). Similar to wingbeat frequency (Figure R4(a-b)), the change of total energy (dE') is more sensitive to d_{Move} as compared with d_{Wing}. For example, when the neighbour birds are far in front ($d_{Wing}>0$), the focal birds have to flap their wings faster ($df_{wb}>0$) and increase their total energy ($dE'>0$) (indicating more power output) compared to the neighbouring birds. This thus indicates that maneuvers along the movement direction require a change of power output, while maneuvers in the wing direction do not.

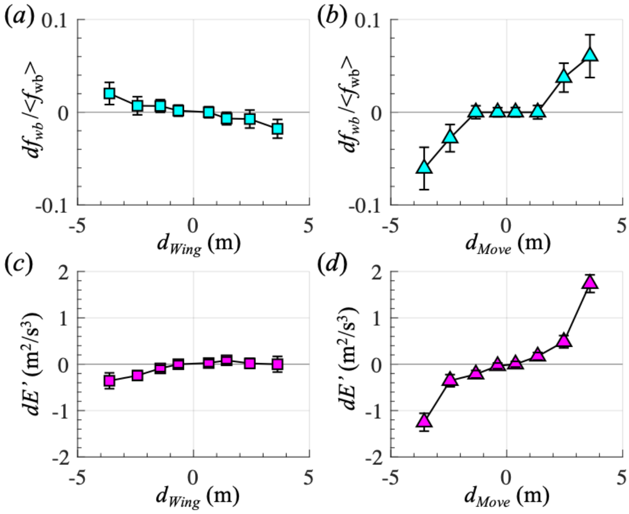


Figure R4. (a-b) df_{wb} as a function of d_{Wing} (a) and d_{Move} (b). (c-d) dE' as a function of d_{Wing} (c) and d_{Move} (d). Here, $df_{wb}>0$ indicates that focal birds flap their wings faster than their neighbours, and $dE'>0$ indicates that focal birds output more mechanical power than neighbours. Results are obtained based on 149,230 samples from 305 isolated pairs.

To reflect these points, we made the following modifications in the revised paper:
- In line 22 of the abstract, the sentence was modified.
- In line 142, we defined how we calculated the total energy *E* and the rate of change of the total energy *E'*.
- The title of section (c) in the Results section was renamed to: “Wingbeat frequency and flight power output”, and the paragraph in section (c) was modified.
- The discussion in lines 267 to 271 was modified.
- The original Figure 7 was modified by the above Figure R4.

Line 284 – The discussion in the results was on how subgroups are elongated in the wing direction; is this also true of the whole group? Inspection of figure S2 seems to show a variety of whole-group bounding box aspect ratios.

Response: The results for the whole group are shown in Figure R5. The entire groups are still elongated in the wing direction (Figure R5), though with the magnitudes of L_{Wing}/L_{Move} being slightly smaller than those of subgroups.

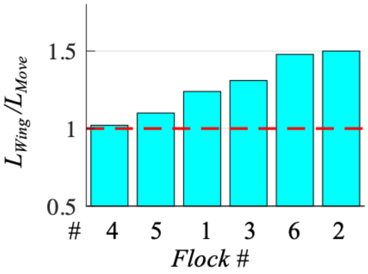


Figure R5. L_{Wing}/L_{Move} of the entire groups for flocks #1 to 6, showing that most flocks are still elongated in the wing direction, similar to subgroups in flocks.

To reflect this point, we now provide Figure R5 as *electronic supplementary material figure S6*, and refer this figure in line 228 as: "...The flocks as a whole are however still elongated in the wing direction (*electronic supplementary material figure S6*), though with a smaller L_{Wing}/L_{Move} as compared to subgroups..."

Line 298 – The physics of bird flight are strongly affected by flight speed; are the social forces similarly affected? The speed range in the pairwise data suggests that you should have enough of a speed range to investigate this and better knit together bird flocking and bird flight physics.

Response: This is a very good question. Using the 149,230 samples from the 305 isolated pairs, we looked at the effect of flight speed on F_{Turn} and F_{Speed}. The results are shown in Figure R6. Clearly, the absolute value of speeding force increases with focal birds' flight speed (Figure R6(b)). However, no clear relation between turning force and focal birds' speed is found (Figure R6(c)).

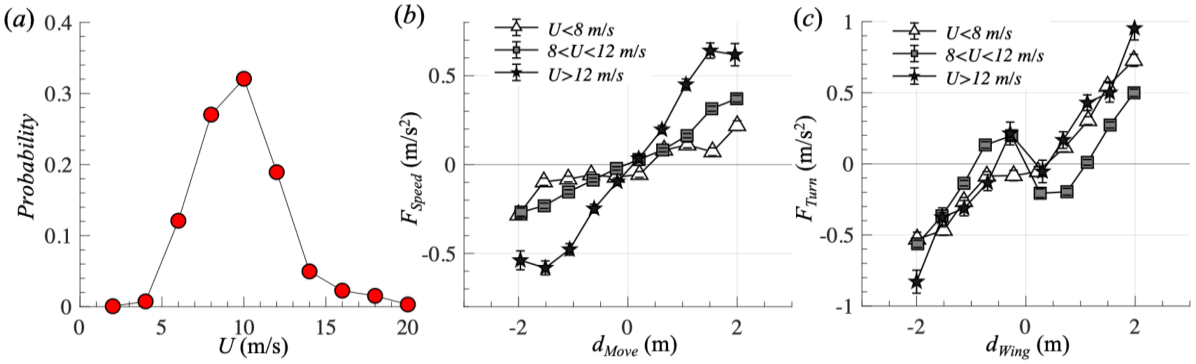


Figure R6. (a) Probability density distribution of focal birds' flight speed (U). (b) Speeding force (F_{Speed}) as a function of d_{Move} at three different flight speed levels of focal birds. (c) Turning force (F_{Turn}) as a function of d_{Wing} at three different flight speed levels of focal birds. Results are obtained from 149,230 samples from the 305 isolated pairs. The three different speed levels (U<8 m/s, 8<U<12 m/s and U>12 m/s) are selected based on the probability density distribution of U. U<8 m/s is located in the low speed region, and U>12 m/s is located in the high speed region. For each line in (b) and (c), the sample size ranges from 24,000 to 80,000. As U increases, F_{Speed} in the region d_{Move}>0 is larger, and F_{Speed} in the region d_{Move}<0 is smaller. Both trends indicate that the strength of the speeding force increases with U.

We now provide Figure R6 as *electronic supplementary material figure S3*, and refer to this figure in line 198 as: "...We also find that $|F_{Speed}|$ increases with the flight speed of focal birds, similar to fish [59], while $|F_{Turn}|$ does not show a clear relationship with speed (*electronic supplementary material figure S3*)...."

Table 1 – The Isolated pairs number of birds is 610 or 710?

Response: The number was corrected to 610.

Appendix B

Dear authors,

Thanks for your revision and thorough response to my comments on the initial version, I found the current manuscript more streamlined and informative. Also, I do find your results very interesting and appreciate the extent to which you've made the underlying data and even some analysis code available for review – I expect this will lead to a better and more widely cited paper in the long run, even if it seems difficult now.

The revision and response did raise a few remaining points that require correction:

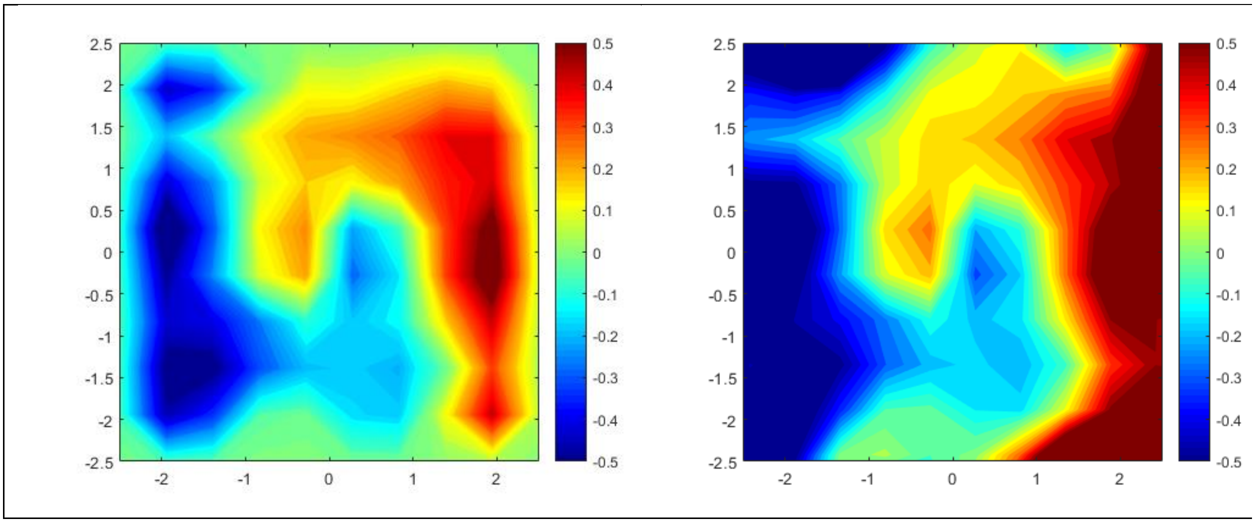
First, standard errors in line plot (e.g. Figs. 3d, 5) should be calculated from the number of birds, not the number of sampled data points. Repeated measurements of the same bird are not independent statistical events.

Second, regardless of what a different set of authors did almost a decade ago, if your results are calculated in a way to forces axial symmetry, you can't then turn around and show both directions as if they are independently measured. Put another way, you introduce your analysis as looking at social forces, and even use F to denote your acceleration measurement, but your results do not show the forces acting on the focal bird. Either put the results in a single quadrant in keeping with your calculations or see if you can create a truly directional map by apportioning force among birds in a pair by considering their single as well as joint accelerations.

I initially asked about your spatial histogram scale size because I had binned with a much finer grid which, given the amount of variation in the dataset, results in much larger local acceleration peaks. I now see that coarse binning is required to reveal the underlying flock trend – the figure generation code was very useful in this regard! However, I also noticed that your figure code for4B and 4C includes some oversights. Specifically, your cell population loop enforces an unpopulated edge all the way around the histogram, such that MATLAB's interpolation layer pulls the values toward zero even though you intend for that to be a null cell. You need to extend your linspaces 2 steps further outward – see below.

Original code (minus some font size changes, etc.) and with countourf() set to 64 levels – Note the border of 0 all the way around the figure	Corrected code that fully populates the border cells from the data.

```
%% figure 4b-c: maps of F_turn and F_speed
% generate 2D grid points
x_edges=linspace(-3.5,3.5,14);
y_edges=linspace(-3.5,3.5,14);
% initialize the focal on grid point as 0
a1=zeros(numel(x_edges),numel(x_edges));
a2=zeros(numel(y_edges),numel(y_edges));
```



Finally, I notice that the underlying effect size of relative bird positions on acceleration (about 0.2 m/s^2 per m distance) is very small compared to the variation in acceleration in your dataset (standard deviation of ~1.5 to 3 m/s^2, depending on direction). Is the attraction effect actually strong enough to keep the flock together given the large natural variability in acceleration? A quick simulation of a 1-D walker suggests it is not, but that simulation assumes successive accelerations are independent of one another and thus doesn't reflect reality particularly well. Does a better simulation show that the effect is strong enough, or is there something like a PI control scheme in place to enhance it? Alternatively, is most of the variation in acceleration probably measurement error accumulated along the path from positions to the difference between 2 second derivatives? If this is the case it would be useful to extend the uncertainty in position calculation (line 109) out to your uncertainty in acceleration.

Appendix C

Response to reviewer

Comment: Thanks for your revision and thorough response to my comments on the initial version, I found the current manuscript more streamlined and informative. Also, I do find your results very interesting and appreciate the extent to which you've made the underlying data and even some analysis code available for review – I expect this will lead to a better and more widely cited paper in the long run, even if it seems difficult now. The revision and response did raise a few remaining points that require correction.

Response: We thank the reviewer for the positive feedback on our revised manuscript. Below is a point by point response to the reviewer's comments.

Comment: First, standard errors in line plot (e.g. Figs. 3d, 5) should be calculated from the number of birds, not the number of sampled data points. Repeated measurements of the same bird are not independent statistical events.

Response: We agree with the reviewer that the data points are not all independent events, and we should not use the total sample size for the calculation of standard error. However, the number of *uncorrelated* data points is larger than the number of birds since d_{Move}, d_{Wing}, F_{Speed} and F_{Turn} measured from a same bird all vary in time (Figure R1). To estimate the statistical uncertainty (rather than any systematic bias) in our measurements, we argue that the proper sample size to use in computing the standard error is the number of uncorrelated samples. We determined the number of uncorrelated data points for each bird trajectory based on the autocorrelation functions $C(\delta t)$ of F_{Speed} and F_{Turn}, where δt is the time lag (Figure R2). The correlation time t_0 is determined as the time when $C(\delta t)$ first goes to 0 (Figure R2). Two data points separated by a time step larger than t_0 are by definition uncorrelated. The total number of uncorrelated data points is thus equal to Nt/t_0, where N is the number of birds and t is the trajectory length. In Table R1, we list values of $60Nt$ (the total number of data points since we recorded data at 60 frames per second and we measure t in seconds), t_0, and Nt/t_0 for isolated pairs and flocks #01 to 06.

To make clear what assumptions we made and calculations we performed, we have added a sentence in the electronic supplementary materials, section "*One-dimensional force curves*", to describe how we calculated the standard errors: "...For each point on the one-dimensional curves, the standard error was calculated using a sample size corresponding to the number of uncorrelated data points..."

Using the number of uncorrelated data points, we re-calculated the standard errors and modified Figures 4d, 5 and 7, in the revised paper and Figure S3 in the electronic supplementary materials. Since the new standard errors increase, in the caption of Figure 4, we deleted the sentence: "...Each point in (d) was calculated by averaging 7,000 to 30,000 samples, and has a standard error smaller than the symbol size..." Additionally, in the captions of Figures 4, 5, 7, and S3, we added the sentence: "...Error bars are standard errors..."

We also added the following sentences in the electronic supplementary materials:

> "...To determine the number of uncorrelated data points measured from each bird, we calculated the correlation functions $C(\delta t)$ of F_{Speed} and F_{Turn}, where δt is the time lag. The correlation time t_0 is determined as the time when $C(\delta t)$ first goes to 0. Two data points separated by a time step larger than t_0 are uncorrelated. The total number of uncorrelated data points is equal to Nt/t_0, where t is the trajectory length. In Table S1, we list values of $60Nt$ (the total number of data points), t_0, and Nt/t_0 for isolated pairs and flocks #01 to 06..."

Table R1 was added as a new Table S1 in the electronic supplementary materials.

We deleted the sentence in the electronic supplementary materials that: "...In this study, for the 305 isolated pairs, we have a total 149,230 data points. For birds flying in large groups (flocks #1 to #6), the number of data points for each group ranges from 8,000 to 64,300..."

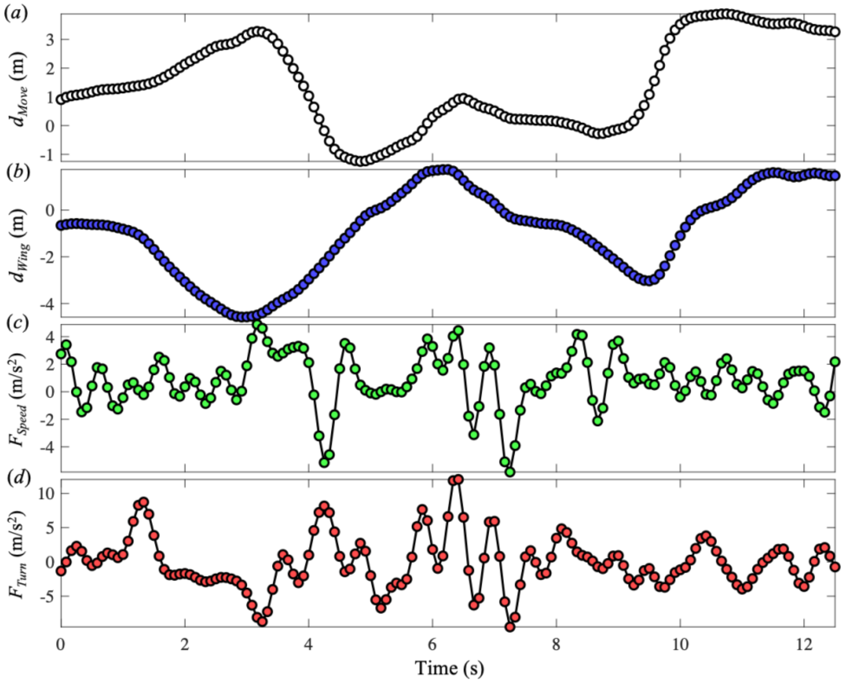


Figure R1. Temporal variation of (a) d_{Move}, (b) d_{Wing}, (c) F_{Speed}, and (d) F_{Turn} for a given focal bird, with its trajectory shown in Figure 1.

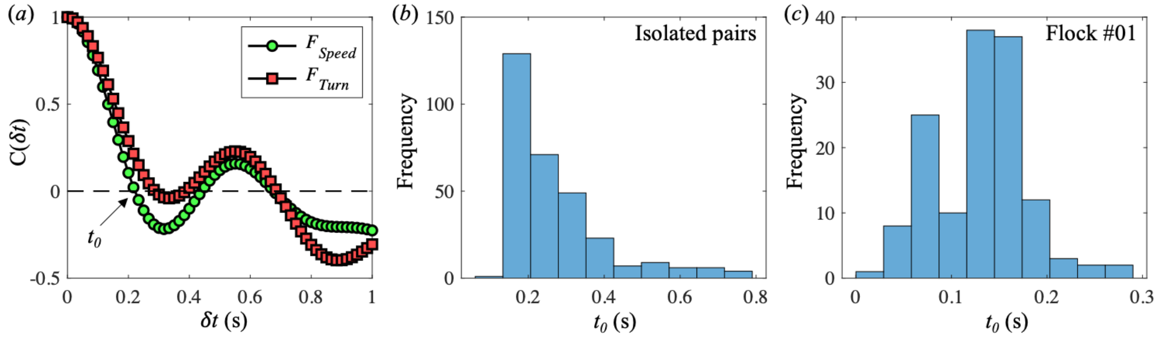


Figure R2. (a) Correlation functions C(δ*t*) of F_{Speed} and F_{Turn} corresponding to the signals shown in Figure R1; (b) Distribution of correlation time t_0 for 305 isolated pairs; (c) Distribution of t_0 for flock #01.

	Isolated pairs	Flocks #01	Flocks #02	Flocks #03	Flocks #04	Flock #05	Flocks #06
60Nt	149,230	64,322	29,090	26,686	23,830	8638	11,124

t_0 (s)	0.27	0.12	0.13	0.14	0.14	0.13	0.15
Nt/t_0	9210	8930	3730	3177	2837	1100	1230

Table S1. The total number of sample points 60Nt, average correlation time t_0, and total number of uncorrelated data points Nt/t_0 for 305 isolated pairs and flocks #01 to 06.

Comment: Second, regardless of what a different set of authors did almost a decade ago, if your results are calculated in a way to forces axial symmetry, you can't then turn around and show both directions as if they are independently measured. Put another way, you introduce your analysis as looking at social forces, and even use F to denote your acceleration measurement, but your results do not show the forces acting on the focal bird. Either put the results in a single quadrant in keeping with your calculations or see if you can create a truly directional map by apportioning force among birds in a pair by considering their single as well as joint accelerations.

Response: In our previous response and in the electronic supplementary materials, we stated that: "...The resulting force maps and force curves were thus forced to be antisymmetric with respect to d_{wing} or d_{move}..." However, upon further reflection, this sentence is inaccurate.

First, for isolated pairs, this sentence is not true if the flight directions of two birds are not the same, since F_{Turn} and F_{Speed} are obtained by decomposing $\boldsymbol{F} = \boldsymbol{a}^{\text{focal}} - \boldsymbol{a}^{\text{neighbour}}$ in a local coordinate system defined based on the flight direction *of the focal bird*. If two birds are flying in different directions, the magnitudes of $|F_{Turn}|$ and $|F_{Speed}|$ measured for the two birds will not be the same.

Second, this sentence is not true for large groups. For large groups, if bird A is the nearest neighbour of a focal bird B, it is not guaranteed that B is the nearest neighbour of A. Therefore, $|F_{Turn}|$ and $|F_{Speed}|$ measured for birds A and B may not be the same.

Therefore, F_{Turn} and F_{Speed} on two sides of the axis are not guaranteed to be symmetrical. We thus removed the sentences in the electronic supplementary materials: "...The resulting force maps and force curves were thus forced to be antisymmetric with respect to d_{wing} or d_{move}. Nevertheless, we present the full force maps and curves (i.e., for both positive and negative values of d_{wing} and d_{move}) for two reasons. Since a neighbouring bird may be found either in front of or behind the focal bird, the full force maps and curves reflect the force distribution for all possible neighbour locations. Additionally, showing the full maps and curves renders qualitive comparison to those reported in fish schools (e.g., Katz *et al.*, 2011) simpler...."

We added the following sentences in the electronic supplementary materials: "...We show the full force maps and curves for the following reasons: (i) F_{Turn} and F_{Speed} on the two sides of the axis are not guaranteed to be symmetric; (ii) a neighbouring bird may be found either in front of or behind the focal bird, and so the full force maps and curves reflect the force distribution for all possible neighbour locations; and (iii) showing the full maps and curves renders qualitative comparison to those reported in fish schools (e.g., Katz *et al.*, 2011) simpler..."

I initially asked about your spatial histogram scale size because I had binned with a much finer grid which, given the amount of variation in the dataset, results in much larger local acceleration peaks. I now see that coarse binning is required to reveal the underlying flock trend – the figure generation code was very useful in this regard! However, I also noticed that your figure code for4B and 4C includes some oversights. Specifically, your cell population loop enforces an unpopulated edge all the way around the histogram, such that MATLAB's interpolation layer pulls the values toward zero even though you intend for that to be a null cell. You need to extend your linspaces 2 steps further outward – see below.

Response: Thanks very much for pointing this out. We have followed the reviewer's suggestion and extended the linspaces, and modified Figure 4 (see Figure R3). The corresponding parts of the code provided in the supplementary material and uploaded in FigShare were also modified.

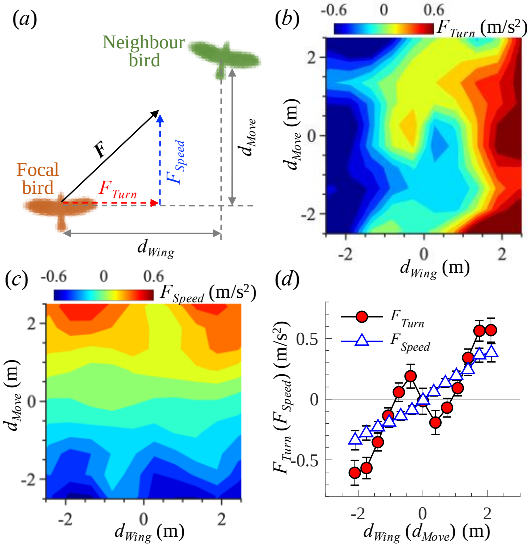


Figure R3. Modified Figure 4.

Finally, I notice that the underlying effect size of relative bird positions on acceleration (about 0.2 m/s^2 per m distance) is very small compared to the variation in acceleration in your dataset (standard deviation of ~1.5 to 3 m/s^2, depending on direction). Is the attraction effect actually strong enough to keep the flock together given the large natural variability in acceleration? A quick simulation of a 1-D walker suggests it is not, but that simulation assumes successive accelerations are independent of one another and thus doesn't reflect reality particularly well. Does a better simulation show that the effect is strong enough, or is there something like a PI control scheme in place to enhance it? Alternatively, is most of the variation in acceleration probably measurement error accumulated along the path from positions to the difference between 2 second derivatives? If this is the case it would be useful to extend the uncertainty in position calculation (line 109) out to your uncertainty in acceleration.

Response: The reviewer raises some interesting questions about flock cohesion here. Ultimately, understanding flock cohesion is thorny issue that really warrants its own in-depth study, particularly given the possibility of non-kinematic effects (as the reviewer alludes to in mentioning something like a PI control scheme). Thus, we feel that this is a topic best saved for future work, with (as the reviewer also implicitly suggests) a substantial modelling component.

That being said, we can provide some answers to the specific questions the reviewer raises here. First, comparing the mean value of the acceleration with the fluctuations is fraught, and must be interpreted with care. For example, the full ensemble of accelerations, from which we compute a standard deviation, includes measurements taken at different points in space *and in time*. Thus, some of the variability we see comes from temporal fluctuations that may be spatiotemporally correlated. More generally, fluctuations are uncorrelated with mean values, and so the size of typical fluctuations does not constrain the mean.

The reviewer is certainly correct that there will be more noise in the acceleration than in the position given that derivatives are a high-pass filter (though this is mitigated to some degree given the numerical scheme we use to estimate derivatives). But if our measurements were dominated by noise, we would not expect to see a coherent trend in the data. The observation of such a trend coupled with the numerical scheme we use suggests to us that the variability in acceleration is likely not just a measurement artefact. As some evidence of this, we show time traces of the acceleration for two birds in Figure R4 below. Even though the acceleration fluctuates, it is relatively smooth, suggesting that noise is not dominant.

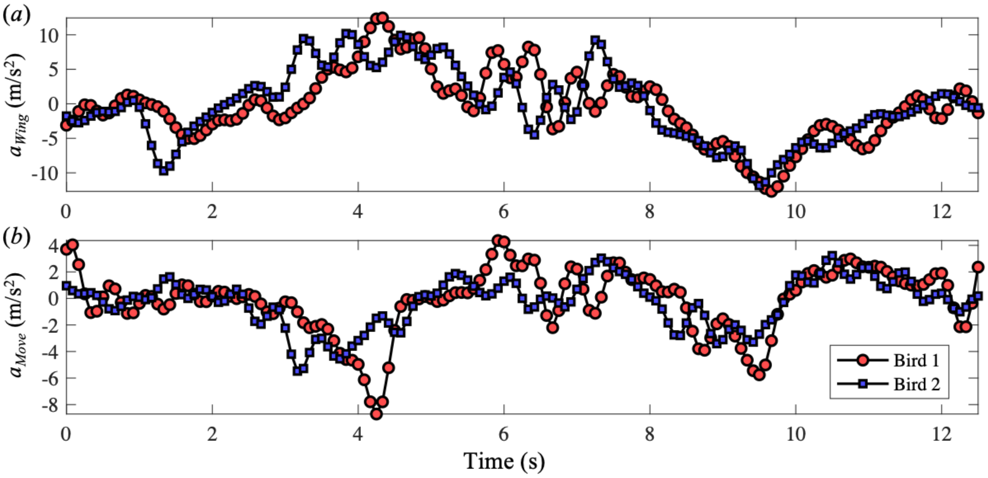


Figure R4. Temporal variations of accelerations in wing and movement directions, a_{Wing} and a_{Move}, corresponding to the trajectories shown in Figure 1.