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Personality composition determines social learning pathways within shoaling fish

Matthew J. Hasenjager, William Hoppitt and Lee A. Dugatkin

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Original submission: 23 February 2020
1st revised submission: 3 August 2020
2nd revised submission: 8 September 2020
Final acceptance: 15 September 2020

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

Review History

RSPB-2020-0399.R0 (Original submission)

Review form: Reviewer 1 (Culum Brown)

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
This is a very interesting paper examining the influence of individual personalities on the spread of novel information (location of a foraging patch) through a group. The network analysis they have employed is comprehensive and cutting edge and suggests that the nearest neighbour metric was not as good as the elective group size metric in estimating transmission probabilities to naïve individuals. Bold individuals were far more likely to act as demonstrators than shy individuals but their role in transmission varied with group composition. Group composition also influenced the likelihood that the group solved the task.
The paper is very well presented and I could only add a few comments here and there to improve the text (see marked pdf).
Overall this MS makes a great contribution to the existing literature.

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?
Acceptable

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

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?
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?
N/A

Is it adequate?
N/A

Do you have any ethical concerns with this paper?
No

Comments to the Author
Please see attached file. (See Appendix A)

Decision letter (RSPB-2020-0399.R0)

01-Apr-2020

Dear Dr Hasenjager:

I am writing to inform you that your manuscript RSPB-2020-0399 entitled "Personality composition determines social learning pathways within shoaling fish" 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,
Dr Robert Barton
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
The two reviewers agree (as do I) that this is a well-designed study addressing an interesting and important issue. However, while reviewer 1 has only minor comments to improve the clarity of the paper, Reviewer 2 raises an important alternative explanation for the results that needs to be given careful consideration. This reviewer also raises concerns as to potential sample size-based limitations for NBDA analysis. These issues will need to be addressed thoroughly before the manuscript can be considered for publication.

Reviewer(s)' Comments to Author:
Referee: 1

Comments to the Author(s)

This is a very interesting paper examining the influence of individual personalities on the spread of novel information (location of a foraging patch) through a group. The network analysis they have employed is comprehensive and cutting edge and suggests that the nearest neighbour metric was not as good as the elective group size metric in estimating transmission probabilities to naïve individuals. Bold individuals were far more likely to act as demonstrators than shy individuals but their role in transmission varied with group composition. Group composition also influenced the likelihood that the group solved the task.
The paper is very well presented and I could only add a few comments here and there to improve the text (see marked pdf).
Overall this MS makes a great contribution to the existing literature.

Referee: 2

Comments to the Author(s)
Please see attached file.

Author's Response to Decision Letter for (RSPB-2020-0399.R0)

See Appendix B.

RSPB-2020-1871.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.
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?
No

Is it clear?
N/A

Is it adequate?
N/A

Do you have any ethical concerns with this paper?
No

Comments to the Author
I thank the authors for addressing my previous comments. I only have some minor comments below which I would like the authors to address before publication:

1) Please make sue the x axes limits on Fig. S5 are the same for these subplot so they are directly comparable.

2) Line 191: It is stated that "Note that although the number of connections varied across sub-networks (e.g., within a mixed group, there are 25 B-S and 20 B-B connections), NBDA estimates social transmission rates per unit of network connection."

I assume this is a typo. In a mixed group of 5 bold and 5 shy individuals, there should be the same number of connections. In fact here, I would use an example from either a bold dominated group, or shy dominated group here, as that would demonstrate more clearly the mismatches between the number of connections in those groups.

3) Line 230: "285 out of 359 individuals solved the task by entering the device."

Please state how many individuals there were in total.

4) Line 236: "The mean (±SD) gap between consecutive solving events was 71.76 ± 117.95 sec (N= 67) in bold-dominated groups, 63.21 ± 118.87 sec (N= 85) in mixed groups, 63.02 ± 91.4 sec (N= 99) in shy-dominated groups."

This does not appear to marry with data from Figure 3. This may be because the mean time is used between consecutive solving events. This distribution (time between consecutive events) is likely to be heavily skewed. Therefore, I suggest using the median or mode time (binned) as a measure of the time between solving events.

Decision letter (RSPB-2020-1871.R0)

25-Aug-2020

Dear Dr Hasenjager:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers' comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Editors have raised some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

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

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

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

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

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

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 (https://royalsociety.org/journals/authors/author-guidelines/#data). Datasets should be deposited in an appropriate publicly available repository and details of the associated accession number, link or DOI to the datasets must be included in the Data Accessibility section of the article (https://royalsociety.org/journals/ethics-policies/data-sharing-mining/). Reference(s) to datasets should also be included in the reference list of the article with DOIs (where available).

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

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

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

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

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

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

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

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

Best wishes,
Dr Robert Barton
mailto: proceedingsb@royalsociety.org

Associate Editor Board Member
Comments to Author:
Both I (associate editor) and one of the original reviewers have carefully reassessed the revised paper, and we both find it much improved. There are just a small number of points of clarification that must be addressed before the paper can be published. Please ensure that you address each point and provide a point-by-point explanation of the changes made to the manuscript.

Reviewer(s)' Comments to Author:
Referee: 2

Comments to the Author(s).
I thank the authors for addressing my previous comments. I only have some minor comments below which I would like the authors to address before publication:

1) Please make sue the x axes limits on Fig. S5 are the same for these subplot so they are directly comparable.

2) Line 191: It is stated that "Note that although the number of connections varied across sub-networks (e.g., within a mixed group, there are 25 B-S and 20 B-B connections), NBDA estimates social transmission rates per unit of network connection."

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Please state how many individuals there were in total.

4) Line 236: "The mean (±SD) gap between consecutive solving events was 71.76 ± 117.95 sec (N= 67) in bold-dominated groups, 63.21 ± 118.87 sec (N= 85) in mixed groups, 63.02 ± 91.4 sec (N= 99) in shy-dominated groups."

This does not appear to marry with data from Figure 3. This may be because the mean time is used between consecutive solving events. This distribution (time between consecutive events) is likely to be heavily skewed. Therefore, I suggest using the median or mode time (binned) as a measure of the time between solving events.

Author's Response to Decision Letter for (RSPB-2020-1871.R0)

See Appendix C.

Decision letter (RSPB-2020-1871.R1)

15-Sep-2020

Dear Dr Hasenjager

I am pleased to inform you that your manuscript entitled "Personality composition determines social learning pathways within shoaling fish" 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 Robert Barton
Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Associate Editor:
Board Member
Comments to Author:
Thank you for your thorough efforts in revising the manuscript. It will make a very useful contribution to the literature.

Appendix A

The manuscript “Personality composition determines social learning pathways within shoaling fish” investigates which personality types of guppies are likely to enter a novel feeding device first, and which individuals copy these demonstrators, based on the personality composition of the group. The authors performed a well-designed experiment where they manipulated the group composition of personality types (shy or bold fish) and then assessed whether this group composition influenced the ‘learning rates’ of other group members. While I found the experiments well designed, I felt the main experimental results were dominated by some sophisticated modelling techniques without any presentation of the raw results in summary statistics or graphical form. Inclusion of this information is essential given these sophisticated modelling approaches. In general, I wondered if the results could simply be explained by a combination of i) bold fish entering the feeding device first and ii) the design of the experiment (e.g. composition of the personality types of individuals in groups) driving the apparent information flow rates between different personality types.

Please see my specific comments below:

1) In general, I wondered whether these modelling approaches were appropriate given the small sample sizes of the experimental data (indeed data across groups appear to be combined in the diffusion analysis to increase power, but this information is only available in the supplementary material). Are there other studies with comparable sample sizes that have used this NBDA analysis?

   In relation to this, how sensitive is the NBDA to certain trials dominating the output of the analysis? For example, if one trial has far more ‘solving events’ than others, but data from all groups are merged into one diffusion analysis, this trial would contribute disproportionally to the analytical output. The robustness of the results could be tested by randomly removing a proportion of trials from the NBDA and rerunning on this smaller sample.

2) Some summary statistics of the experiment would be beneficial. Which personality types entered the feeding device, on average, first? What was the mean time difference between different individuals entering the feeding device? At what rate did uninformed individuals enter the feeding device as a function of the group composition (a survival-type plot here would be useful). Further, some description of how the fish were interacting with the feeder in the experiment would be beneficial to the reader. Which individuals consumed the blood worm? Did all individuals feed on the bloodworm?

3) Please provide some graphically presentation of the number of individuals that solved the task for bold-dominated, mixed, and shy-dominated groups. What was the average number of solvers per group? How did this vary between groups? How did the number of times a fish entered the feeding device vary between individuals in the group? Did this vary as a function of their boldness?

4) How did body size relate to boldness scores? Please report.

5) How does the NBDA analysis account for difference in number of different personality types, and hence the number of connections between different personality types? The authors suggest that in groups of bold fish (8 bold to 2 shy fish), learning is promoted to a greater extend in bold individuals. However, there are clearly more connections between bold-bold individuals in these bold dominated groups. Does this asymmetry not increase the likelihood of finding, for example, bold individuals appearing to have their learning promoted by others ($S_{B/S \rightarrow B} > S_{B/S \rightarrow S}$)?

Similarly, there is clearly far less power to detect an effect of shy individuals promoting learning in bold fish in bold dominated groups (there are only two shy fish in these groups). Could this not drive the pattern that the personality type of the demonstrator (shy or bold) does not influence the learning rate of the observer in these groups?

An argument against this could be that the authors indeed detect bold individuals are important demonstrators in groups of shy fish, but again, the likelihood of finding that shy fish copy bold individuals is enhanced in these shy dominated groups.

In general, I wonder if these results can simply be explained by bold fish entering the feeding device first (unsurprisingly), with the make-up of the group composition (whether groups are dominated by shy or bold individuals) driving the apparent "information flow rates" between individuals. Indeed, in mixed groups, I note that the undifferentiated social learning pathway strength of support (0.375) is practically equivalent to the '*s depends on demonstrator boldness'* strength of support (0.39). How can the authors assert, therefore, that the boldness of informed demonstrators affects social learning rates in these mixed groups? It appears that there is practically equivalent evidence that the social learning rates do not depend on either the boldness of the demonstrator or the observer in mixed groups.

6) Why are there identical confidence intervals in Table 2 for different social transmission rates?

Minor Points:

1) Line 261: It is not clear what "these groups" refers to here. Does this refer to all types of groups, or just mixed and shy dominated?

2) Line 262: It is unclear how the statement "Together, these findings indicate that the dynamics of information flow were similar within bold- and shy-dominated groups, with bold demonstrators more strongly accelerating the rate at which other group members solved the task than shy demonstrators" is inferred. Please can the authors expand? This is particularly confusing as in the discussion (line 310), the authors suggest this effect only occurs within mixed and shy-dominated groups.

3) Line 265: It is unclear where the value of 2.39 comes from. I cannot see how this relates to the figures in Table 2.

4) How many times was the experimental protocol (i.e. days 1-5) repeated? Please add details.

Appendix B

Associate Editor
Board Member: 1
Comments to Author:
The two reviewers agree (as do I) that this is a well-designed study addressing an interesting and important issue. However, while reviewer 1 has only minor comments to improve the clarity of the paper, Reviewer 2 raises an important alternative explanation for the results that needs to be given careful consideration. This reviewer also raises concerns as to potential sample size-based limitations for NBDA analysis. These issues will need to be addressed thoroughly before the manuscript can be considered for publication.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)

This is a very interesting paper examining the influence of individual personalities on the spread of novel information (location of a foraging patch) through a group. The network analysis they have employed is comprehensive and cutting edge and suggests that the nearest neighbour metric was not as good as the elective group size metric in estimating transmission probabilities to naïve individuals. Bold individuals were far more likely to act as demonstrators than shy individuals but their role in transmission varied with group composition. Group composition also influenced the likelihood that the group solved the task.

The paper is very well presented and I could only add a few comments here and there to improve the text (see marked pdf).

Overall this MS makes a great contribution to the existing literature.

**Thank you! We were pleased to see your interest in our manuscript. We have sought to address all of your comments/questions, which we detail below.*

L45: see for example: https://academic.oup.com/beheco/article/25/1/95/222867

**We now allude to this example and include the suggested reference (L43-44).*

L52: a bit too much methody- type info in here for my likeing

**We have streamlined this paragraph (L47-55) to limit the methodological details here.*

L82: A note to self, and the authors, it would be nice to see a distribution of the boldness scores.

**We now include this information in Figure S2 and direct readers to it at L93-95.*

L90: n = ?

**The number of individuals tested is now indicated at L93-95.*

L93: wait a tick, what about repeatability of the boldness assay?

**Thanks for pointing out this potential source of confusion. We now indicate early on at L77-78 that we formally evaluated the repeatability of boldness scores, in addition to using the cut-offs to label individuals as bold or shy.*

L112: 4 is a decent length. Id bung a ref in here to justify that. Im sure you'll find one from Magurran

L115: I think you are talking about elective group size. Seghers (and me as well) have use that definition in the past. blast from the past...
Behavioral Ecology and Sociobiology 41 (1), 61-68

**We have included the following reference (L109, L111) both to justify our definition of shoaling proximity and use of the elective group size measure: Pitcher, T. J. & Parrish, J. K. 1993. Functions of shoaling behaviour in teleosts. In: Behaviour of Teleost Fishes (Ed. by T. J. Pitcher), pp. 363-439. London: Chapman & Hall.*

L123: did a lot of fish enter?

**Most fish (285/359) entered the device at least once during the experiment. Previously, this important information was provided only at the very end of the results! We now rectify this oversight by providing it much earlier (L230), along with additional descriptive information about how fish interacted with the task (see responses to Reviewer 2).*

L130: repeatability... check. Jolly good

**Based on your earlier comment, we now alert readers earlier in the manuscript that this analysis was performed (L77-78).*

L137: suggest you use "elective group size"

**Throughout the manuscript, we have replaced "subgroup size" with "elective group size".*

L139: hmmm the loss of one fish means the probability of encountering the novel patch by chance alone declines.
To be double sure about this try running the stats without this group.

**We have repeated the NBDA, as well as the other statistical analyses, with this group removed. Results were essentially identical to those reported in the manuscript, with one exception: the confidence interval for the difference in social transmission rate between bold and shy learners in bold-dominated groups now included 0 (difference estimated at 1.2, 95% CI = -0.2, 2.9). However, given that removal of this group led to a ~10% reduction in sample size for the bold-dominated groups (i.e. removal of 8 out of 78 solvers), increased*

uncertainty in parameter estimates is not unusual. Furthermore, we have little reason to suspect that this finding of increased social learning rates for bold individuals in bold-dominated groups is simply an artifact derived from including this group—if anything, its composition is shifted slightly towards that of mixed and shy-dominated groups (i.e. bold individuals were slightly less over-represented in this group relative to other bold-dominated groups). Nevertheless, we include these results in the supplementary material (Tables S6-S11) and direct readers to them at L123-125.

L142: what does standardized mean? Do you mean standard length to the caudal peduncle?

**Body length was indeed measured as standard length (snout to the base of the caudal peduncle) as noted at L90-92. Our use of standardized in regard to the statistical analysis referred to standardizing values by first subtracting the mean and then dividing by the standard deviation. However, we have slightly modified our treatment of body length in the statistical analysis by now centering values according to the mean body length within each group. This was done both because we size-matched within (but not across groups) and treating the variable in this way led to improvements in model fit based on inspection of residuals.*

L151: how and why? what is the impact of removing the outlier?

**Entry rate was initially calculated as the number of times an individual entered the device divided by the time remaining in the trial once it was informed. One individual first entered the device 3.3 sec before the end of the trial, resulting in an estimated entry rate of 1/(1200-1196.7) = 0.303 entries per sec (18.18 entries per min). For reference, the next highest entry rate was 1.84 entries per min and the average entry rate of informed individuals (not counting the outlier) was 0.56 entries per min. Inspection of the model residuals indicated that the assumption of normality was clearly violated when including this individual, so it was removed.*

**However, upon further reflection, this earlier analysis may not have been the most appropriate way to handle this data. Rather, number of entries during the trial can be treated as a discrete count, with the time remaining in the trial once an individual is informed included as an offset. Treating the analysis in this way means we can include this individual without it having a disproportionate influence relative to others. We also note that the results for this analysis are comparable to our initial model (where entry rate was analyzed using a Gaussian distribution in an LMM). There was little evidence that individual personality, group composition, nor their interaction influenced the number of times informed individuals entered the device, but relatively large individuals tended to enter the device slightly more often (L273-278; Table S5).*

L327: good point. Shame you didnt measure EGS during the experiment

**We agree. In principle, it may be possible to obtain some of this data by returning to the video recordings, but changes in elective group size directly in response to introducing the novel device may also be confounded with any changes resulting from group members*

beginning to discover the presence of food within it. Ideally, we would have run additional trials alongside where groups were presented with the device with no food present. Unfortunately, this experiment was conducted several years ago and the lead author (MJH) is no longer at the institution where this work was carried out, limiting our ability to carry out additional experimental work.

Referee: 2

The manuscript "Personality composition determines social learning pathways within shoaling fish" investigates which personality types of guppies are likely to enter a novel feeding device first, and which individuals copy these demonstrators, based on the personality composition of the group. The authors performed a well-designed experiment where they manipulated the group composition of personality types (shy or bold fish) and then assessed whether this group composition influenced the 'learning rates' of other group members. While I found the experiments well designed, I felt the main experimental results were dominated by some sophisticated modelling techniques without any presentation of the raw results in summary statistics or graphical form. Inclusion of this information is essential given these sophisticated modelling approaches. In general, I wondered if the results could simply be explained by a combination of i) bold fish entering the feeding device first and ii) the design of the experiment (e.g. composition of the personality types of individuals in groups) driving the apparent information flow rates between different personality types.

**Thank you for your thoughtful feedback. You raise several important points which we have addressed in our revised manuscript. We also now provide important summary statistics and graphical presentations of key patterns in our data (e.g. the number of solvers per group).*

Please see my specific comments below:

1) In general, I wondered whether these modelling approaches were appropriate given the small sample sizes of the experimental data (indeed data across groups appear to be combined in the diffusion analysis to increase power, but this information is only available in the supplementary material). Are there other studies with comparable sample sizes that have used this NBDA analysis?

In relation to this, how sensitive is the NBDA to certain trials dominating the output of the analysis? For example, if one trial has far more 'solving events' than others, but data from all groups are merged into one diffusion analysis, this trial would contribute disproportionally to the analytical output. The robustness of the results could be tested by randomly removing a proportion of trials from the NBDA and rerunning on this smaller sample.

NBDA has successfully been employed using captive groups with as few as 5 individuals—e.g., starlings (Sturnus vulgaris) (Hoppitt W et al. (2010) J. Theor. Biol.* ***263**, 544-555)—though larger groups generally offer more power to detect social learning. The overall number of individuals and group sizes used in our study compare favorably to other*

applications of NBDA that have used this multi-network partitioning approach. For reference, we had 35 groups of 10 individuals and 1 group containing 9 individuals (359 individuals total). Across all groups, 285 fish entered the device at least once (our metric for solving). Below, we have included the corresponding sample sizes, group sizes, and number of solvers for several previous studies that have used a multi-network NBDA:

- *Atton N et al. (2014) Proc. R. Soc. B **281**, 20140579: Seven captive groups containing 10 stickleback fish each; of these 70 individuals, 39 solved the task. Each group was composed of two subgroups of 5 fish that were familiar with one another, but not with members of the other subgroup. A multi-network NBDA was used to estimate separate social transmission rates for familiar and unfamiliar pairs.*
- *Farine DR et al. (2015) Curr. Biol. **25**, 2184-2188: Two aviaries of captive zebra finches, with each aviary containing multiple family groups. Aviary 1 contained 29 finches and aviary 2 contained 34. Across these 63 individuals, 39 solved the foraging task. The full network was partitioned into 8 sub-networks (e.g. juvenile to juvenile, adult to juvenile, adult to adult connections, etc.) The primary question related to potential differences in social transmission biases between juveniles that were either treated with cortisol or not, meaning 6 separate social transmission rates were estimated depending on the demonstrator identity (parent, non-parent adult, juvenile) and the observer identity (CORT-treated or control juvenile). For these comparisons, there were 14 CORT-treated and 14 control juvenile solvers across the two aviaries.*
- *Farine DR et al. (2015) Proc. R. Soc. B **282**, 20142804: Mixed-species songbird populations for two spatially distinct areas. In area 1, the network contained 93 individuals and in area 2, the network contained 81 birds. Three to four diffusions were carried out in each area. Across all trials and areas, there were 103 discovery events. The networks were partitioned such that separate social transmission rates were estimated for conspecific and heterospecific network connections.*
- *Canteloup C et al. (2020) Nat. Comm. **11**, 459: Two groups of wild vervet monkeys containing 28 and 12 individuals respectively. There were 19 and 10 solving events in these groups. A multi-network NBDA was used to estimate differences in social transmission rate between high-ranking vs. low-ranking demonstrators; male vs. female demonstrators; within and among age classes; and between kin vs. non-kin (as well as between different categories of kin).*

**To summarize, our group sizes (10 fish per group) are comparable (albeit on the lower end) to many of the above studies. However, we were able to include many more replicate groups (36 vs. 2–7 groups) and individuals overall than previous studies.*

**As you noted, we employed a stratified OADA (order-of-acquisition diffusion analysis), in which all groups are included within a single network and all between-group connections are set to 0. This approach is common in studies employing NBDA as it offers key advantages (described below) of both an unstratified OADA and a time-of-acquisition diffusion analysis (TADA)—indeed both the Atton et al. (2014) and Canteloup et al. (2020) studies described above used a stratified OADA.*

**First, when using TADA, researchers must make assumptions about the shape of the baseline rate function that describes how the rate of learning changes over time, which can result in misleading inferences if the baseline function is mis-specified. Conversely, when using OADA, the shape of the baseline rate function is left unspecified and is simply assumed to be the same for all individuals in the diffusion (though potentially modified by other variables, such as body size or sex). As such, the stratified OADA used here assumes that the same baseline rate function (whatever that may be) applies to all individuals across all groups, which we assumed to be reasonable given the common population origin and standardized testing conditions in our experiment. By including group composition, personality type, and body size in the analysis, we could also allow for these factors to modify baseline learning rates.*

**Second, a stratified OADA is also advantageous because (as with TADA) it takes into account information about the relative timing of solving events across separate groups that can be used to infer social transmission (an unstratified OADA ignores this information). As an example, imagine an experiment with three groups. All individuals in group 1 solve the task at the start of the experiment, all in group 2 solve in the middle, and all in group 3 solve at the end. This pattern is consistent with social learning promoting rapid uptake of the solution once it is discovered in each group but would not be detected using a standard OADA.*

**For these reasons, we felt that a stratified OADA would be the best option for these data. We now expand on our reasoning in the electronic supplementary material, as well as briefly summarize this reasoning in the main text (L164-169).*

**With regards to a disproportionate number of solvers in one group potentially skewing the analysis, we do not believe this is likely to apply to our findings. Save for the one group in which an individual died, all groups contained the same number of individuals, limiting the potential for one group to have disproportionately more solvers than others. Moreover, in groups in which the task was solved, a similar number of individuals tended to solve the task (mean number of solvers per group: bold-dominated = 7.1; mixed = 8.7; shy-dominated = 9.3). Indeed, a majority of the groups in which the task was solved contained at least 7 solvers (8/11 bold-dominated groups, 10/11 mixed groups, and 12/12 shy-dominated groups). This information is now presented in graphical form in Figure 2 and summarized at L230-233.*

**Nevertheless, to evaluate the robustness of our social transmission rate estimates, we randomly removed 2 groups from each group composition and re-ran the top-ranked model. This procedure was carried out 1000 times. We then compared the parameter estimates from this model (using the complete dataset) with the distribution of values generated by our randomization procedure. This information is provided in Figure S5. As can be seen, the observed values do not significantly differ from those obtained from the randomizations. In addition, differences in social transmission rates were maintained in the randomized distributions. For example, in mixed and shy-dominated groups, the upper estimated limit for social transmission from shy demonstrators (the right tail in panel d) shows little overlap with the estimated lower limit for bold demonstrators' social transmission rate (the left tail*

in panel c). We now describe the rationale and present the results of this randomization test in the electronic supplementary material after introducing the stratified OADA.

2) Some summary statistics of the experiment would be beneficial. Which personality types entered the feeding device, on average, first? What was the mean time difference between different individuals entering the feeding device? At what rate did uninformed individuals enter the feeding device as a function of the group composition (a survival-type plot here would be useful). Further, some description of how the fish were interacting with the feeder in the experiment would be beneficial to the reader. Which individuals consumed the blood worm? Did all individuals feed on the bloodworm?

**Thank you for this excellent suggestion. We now provide this information at the start of the Results (L230-242). Briefly, there was little indication that bold individuals were disproportionately more likely to be the first to solve device in each group; the first solver was bold in 8/11 bold-dominated groups, 7/11 mixed groups, and 2/12 shy-dominated groups that solved the task. The mean gap between consecutive first entries was ~72 sec in bold-dominated groups and ~63 sec in mixed and shy-dominated groups.*

**The NBDA itself is essentially a modified survival analysis that models the rate at which uninformed individuals learn a target behavioral pattern. To aid in visualizing this information, we now include Figure 3 that plots the proportion of individuals across all groups that have solved the task over time as a function of group composition. On this figure, we also indicate the solving events for a subset of representative groups to illustrate how solving events tended to be clustered in time within groups (consistent with socially influenced learning). We considered including this latter information for all groups, but felt it made the figure much too busy to be easily interpretable.*

**Finally, we have included information on how many individuals fed on the bloodworms and how rapidly they began to do so (L238-242). Nearly all (283 out of 285) individuals that solved the device also fed on the bloodworms—264 of these individuals began feeding during their first visit inside the device. The mean latency from initial entry to first feeding strike was 11.1 sec for bold individuals and 14.4 for shy individuals.*

3) Please provide some graphically presentation of the number of individuals that solved the task for bold-dominated, mixed, and shy-dominated groups. What was the average number of solvers per group? How did this vary between groups? How did the number of times a fish entered the feeding device vary between individuals in the group? Did this vary as a function of their boldness?

**We now include Figure 2, which depicts the proportion of individuals within each group that solved the task as a function of group composition. Alongside this figure, we also now include the mean number of solvers per group and range for each group composition at L230-233.*

**At L273-274, we have included the average rate of entry into the device for informed individuals. We also now include Figure S3, which visualizes variation in entry rates within and across groups. Finally, our analysis suggests that individual variation in entry rate was*

not explained by variation in boldness—i.e. bolder individuals did not enter the device more frequently than shy individuals (L274-277; Table S5).

4) How did body size relate to boldness scores? Please report.

**There was some evidence of a weak positive correlation between body size and mean boldness score (r = 0.10, p = 0.06, n = 359), meaning larger fish tended towards shyness. We now include this information at L247-250. We also note that body size was included as an explanatory variable in all statistical analyses alongside boldness.*

5) How does the NBDA analysis account for difference in number of different personality types, and hence the number of connections between different personality types? The authors suggest that in groups of bold fish (8 bold to 2 shy fish), learning is promoted to a greater extend in bold individuals. However, there are clearly more connections between bold-bold individuals in these bold dominated groups. Does this asymmetry not increase the likelihood of finding, for example, bold individuals appearing to have their learning promoted by others (SB/S ® B > SB/S ® S) ?

Similarly, there is clearly far less power to detect an effect of shy individuals promoting learning in bold fish in bold dominated groups (there are only two shy fish in these groups). Could this not drive the pattern that the personality type of the demonstrator (shy or bold) does not influence the learning rate of the observer in these groups?

An argument against this could be that the authors indeed detect bold individuals are important demonstrators in groups of shy fish, but again, the likelihood of finding that shy fish copy bold individuals is enhanced in these shy dominated groups.

In general, I wonder if these results can simply be explained by bold fish entering the feeding device first (unsurprisingly), with the make-up of the group composition (whether groups are dominated by shy or bold individuals) driving the apparent "information flow rates" between individuals. Indeed, in mixed groups, I note that the undifferentiated social learning pathway strength of support (0.375) is practically equivalent to the '*s depends on demonstrator boldness'* strength of support (0.39). How can the authors assert, therefore, that the boldness of informed demonstrators affects social learning rates in these mixed groups? It appears that there is practically equivalent evidence that the social learning rates do not depend on either the boldness of the demonstrator or the observer in mixed groups.

**Thank you for these comments. We agree that these are important points to consider when interpreting our results and we now address these in the manuscript.*

**NBDA estimates the rate of social transmission per unit of network connection—in the case of the group-membership networks, this is equivalent to "per informed group member" as all individuals within a group are assumed to be equally socially connected. Thus, although there are more bold-bold connections in bold-dominated groups than there are bold-shy or shy-shy connections, social transmission rates are estimated on a common scale (per connection), allowing for comparison despite mismatches in the total number of connections. Moreover, even if this was not the case, it is not clear why such an imbalance*

would make it more likely to find in bold-dominated groups that demonstrators promote learning to a greater degree in bold individuals rather than bold demonstrators promoting learning in others. As you noted, in shy-dominated groups, we did not find evidence for the corresponding effect (that is, higher social learning rates for shy observers). Rather, social influence per unit social connection was stronger for bold demonstrators than shy ones in shy-dominated groups. We have included L191-196 to clarify how NBDA estimates social transmission rates and why mismatches in the number or strength of connections is not necessarily an issue.

**You are correct, however, that mismatches in the number of connections can decrease power to detect social effects in some circumstances. For example, within a bold-dominated group, there are 72 incoming connections to bold individuals and only 18 incoming connections to shy individuals, which could result in greater uncertainty and wider confidence intervals for social transmission rates estimated for the latter. Yet model-averaged 95% CI did not overlap with zero for either parameter (Table 2), nor for the estimated difference between them (L298-299), indicating that despite a potential reduction in power, we still have good evidence for our reported effects. Similarly, despite potentially greater uncertainty associated with the effectiveness of bold demonstrators (relative to shy demonstrators) in mixed and shy-dominated groups, the model-averaged 95% CI provides strong evidence for a difference between these effects (L307-310). Note that because mixed and shy-dominated groups were essentially treated as one group composition for this comparison (i.e. social transmission rates were constrained to be equal across these group compositions), the asymmetry in number of outgoing connections from bold demonstrators as opposed to shy ones was less pronounced than if shy-dominated groups were considered on their own.*

**We found little evidence to suggest that our findings were simply driven by differences between personality types in the latency or propensity to enter the device. The NBDA indicates that bold and shy individuals did not differ in their asocial learning rates, meaning bold individuals were not any quicker to solve the task on their own than shy individuals (Table 3). Likewise, bold and shy fish did not differ in how likely they were overall to solve the task (L265-268), nor were bold individuals disproportionately more likely to be the first in their group to enter the device (L234-236). For example, in 10 out of 12 shy-dominated groups, the first individual to enter the device was shy. Our analysis of entry rates also suggests that bold demonstrators did not enter the device more often than shy demonstrators (L273-278). Taken together, these findings indicate that the results of the NBDA are not simply an artifact generated from bolder fish being more likely to enter the device first, lending support to our interpretation that they reflect personality-based differences in social influence that shift according to group composition. We now include L402-414 in the discussion where we address this possible alternative explanation and summarize the above points.*

**Finally, you are correct that the evidence for differences in demonstrator effectiveness is weaker in mixed groups, with uniform social transmission rates across all types of social connection receiving nearly as much support. If patterns of social influence shift according to group composition, then mixed groups may represent an intermediate state between bold- and shy-dominated groups. This is supported by Table 1: in mixed groups, support for*

personality differences in both observer learning rate and demonstrator effectiveness are intermediate between bold- and shy-dominated groups. Within mixed groups, an effect of bold demonstrators more effectively transmitting information may have been offset in part by higher social learning rates for bold individuals, resulting in increased support for uniform social transmission rates. The model-averaged estimates presented in Table 2 also lend support to this interpretation—although the main difference is between bold vs. shy demonstrators, social learning rates were also higher for bolder individuals when comparing within demonstrator classes (e.g. sS->B is greater than sS->S, while sB->B is greater than sB->S). Nevertheless, the fact remains that evidence for an effect of demonstrator boldness on social transmission rates is weaker in mixed groups, which we now prominently state (L310-311). We also include L363-370, where we discuss the possible explanation for this finding discussed above.

6) Why are there identical confidence intervals in Table 2 for different social transmission rates?

**Model-averaged estimates for social transmission rate were obtained using all 1856 candidate models that included the group-membership network. However, to obtain the confidence intervals for s parameters across this same set would be prohibitively time-consuming. This is because confidence intervals tend to be highly asymmetric for social transmission parameters, necessitating the use of profile likelihood techniques which require manual calculation of the upper and lower bounds for each social transmission rate within each model.*

**As a compromise, we instead calculated model-averaged confidence intervals conditional on the set of models that included the best-supported social transmission pathway—that is, within bold-dominated groups, social transmission rates differed for bold vs. shy observers, whereas within mixed and shy-dominated groups, social transmission rates varied depending on demonstrator boldness. In addition, the best-supported pathway constrained social transmission rates to be equal across mixed and shy-dominated groups. These constraints explain the identical confidence intervals reported in Table 2.*

**We have now added L333-337 clarifying why these identical confidence intervals occur. In addition, we now highlight the best-supported transmission pathway in Table S1 to aid readers in better visualizing the above constraints that underlie the confidence intervals reported in Table 2.*

Minor Points:

1) Line 261: It is not clear what “these groups” refers to here. Does this refer to all types of groups, or just mixed and shy dominated?

**This has been clarified to indicate just mixed and shy-dominated groups (L306).*

2) Line 262: It is unclear how the statement “Together, these findings indicate that the dynamics of information flow were similar within bold- and shy-dominated groups, with bold demonstrators more strongly accelerating the rate at which other group

members solved the task than shy demonstrators" is inferred. Please can the authors expand? This is particularly confusing as in the discussion (line 310), the authors suggest this effect only occurs within mixed and shy-dominated groups.

**We are embarrassed to say this was a typo. It should have read "mixed and shy-dominated groups" (L306-307). Many thanks for catching this!*

3) Line 265: It is unclear where the value of 2.39 comes from. I cannot see how this relates to the figures in Table 2.

**These values (L299), as well as the values reported at L309-310, are model-averaged estimates and confidence intervals of differences in social transmission rates (e.g. social learning rates of bold vs. shy observers), conditional on the 16 models that included the best-supported social transmission pathway (indicated in bold in Table S1). As such, while they are related to the values reported in Table 2, they cannot be directly obtained from them. We have clarified that these are model-averaged estimates (L298 & L309) and indicate how they were obtained at L211-214.*

4) How many times was the experimental protocol (i.e. days 1-5) repeated? Please add details.

**In total, this procedure was completed 27 times to generate the 36 experimental groups; occasionally, we were able to construct and test two experimental groups simultaneously. We now include this information at L126-127.*

Appendix C

Associate Editor Board Member
Comments to Author:
Both I (associate editor) and one of the original reviewers have carefully reassessed the revised paper, and we both find it much improved. There are just a small number of points of clarification that must be addressed before the paper can be published. Please ensure that you address each point and provide a point-by-point explanation of the changes made to the manuscript.

***We were pleased to hear that you and our referee were satisfied by the revisions to our manuscript. We have addressed the remaining comments and explain these changes below. In addition to these changes, we have made a small number of minor modifications.*

- *To enhance interpretability of the results in Tables S3-S8, we have rerun these models with mean-centred categorical input variables; we now note this at L147-148.*
- *We have slightly modified elements of Figures 2 and 3 to enhance their presentation (e.g. font size, axis tick marks, line thickness, etc.).*
- *For the mixed effects models, likelihood ratio tests for the effect of body length are now made using models that include the interaction term between group composition and individual personality. This resulted in minor adjustments of test statistics and p-values (L255, L268, L282).*
- *To maintain consistency with other instances in which p-values lie between 0.05 and 0.10 (e.g. L256-259), we now indicate in the main text that there was weak evidence for an effect of individual personality on the number of times fish entered the device (L279-282). The Discussion was adjusted accordingly (L383-386; L417-419).*

Finally, we confirm that we have uploaded our data and R code to the Dryad Digital Repository. This information is now included in our Data Accessibility statement and References.

Reviewer(s)' Comments to Author:

Referee: 2

Comments to the Author(s).
I thank the authors for addressing my previous comments. I only have some minor comments below which I would like the authors to address before publication:

1) Please make sue the x axes limits on Fig. S5 are the same for these subplot so they are directly comparable.

***We have made the requested change. We have also changed it so that the y-axes are the same across panels.*

2) Line 191: It is stated that “Note that although the number of connections varied across

sub-networks (e.g., within a mixed group, there are 25 B-S and 20 B-B connections), NBDA estimates social transmission rates per unit of network connection."

I assume this is a typo. In a mixed group of 5 bold and 5 shy individuals, there should be the same number of connections. In fact here, I would use an example from either a bold dominated group, or shy dominated group here, as that would demonstrate more clearly the mismatches between the number of connections in those groups.

***As individuals are not permitted to link to oneself, the numbers stated above are accurate. Put another way, a bold individual in a mixed group has 9 outgoing connections—one to each of the 5 shy group mates and one to each of the other 4 bold group mates. Across the 5 bold individuals, there are then 25 edges that originate at a bold fish and terminate at a shy one, but only 20 edges from bold to other bold individuals. Of course, bold and shy fish in mixed groups possess equal numbers of connections when directed edges that originate at shy individuals are also taken into account.*

***Nevertheless, we agree that this point can be more clearly made using either the bold- or shy-dominated groups as an example. We have modified L193 accordingly.*

3) Line 230: "285 out of 359 individuals solved the task by entering the device."

Please state how many individuals there were in total.

***We have made the requested change (L231).*

4) Line 236: "The mean (±SD) gap between consecutive solving events was 71.76 ± 117.95 sec (N= 67) in bold-dominated groups, 63.21 ± 118.87 sec (N= 85) in mixed groups, 63.02 ± 91.4 sec (N= 99) in shy-dominated groups."

This does not appear to marry with data from Figure 3. This may be because the mean time is used between consecutive solving events. This distribution (time between consecutive events) is likely to be heavily skewed. Therefore, I suggest using the median or mode time (binned) as a measure of the time between solving events.

***Thank you for this suggestion. We now present the medians and interquartile ranges at L237-240.*