

Dear Philosophical Transactions editorial committee and referees,

Please find enclosed our thoroughly revised manuscript MS RSTB-2017-0018.R1, retitled “*Eco-evolutionary dynamics, density-dependent dispersal, and collective behavior: implications for salmon metapopulation robustness*”. Below, we individually address all of the comments from the editors and two referees. We have made extensive changes to our manuscript, and have done our best to address all of the concerns that were raised regarding both our approach and issues regarding our formulation of the eco-evolutionary dynamics. We want to acknowledge that our original formulation was incorrect, as was pointed out by both referees, thank both for revealing and pointing out these errors. The model described in this revision has been corrected based on the constructive referees’ comments and we hope you agree that the manuscript is markedly improved.

One important result of these corrections has revealed that our base model is very similar, except for a few details in the functions controlling growth and mortality, as the model proposed by Ronce and Kirkpatrick (as was suggested by one of the referees). To this end, we have reformulated our approach to concentrate on how including density-dependent straying changes the expectations of the original density-independent model and by doing so more squarely aligns with the theme issue. Importantly, our model formulation also makes the same assumptions and approximations as those introduced by Ronce and Kirkpatrick, where it is explicitly shown that these approximations do not meaningfully impact the dynamics. We use this as justification for our approach, but also include a supplementary section where we explore some of the ramifications of the approximation used in the model.

We believe that our revision is greatly improved by the detailed suggestions and critiques delivered to us by the editors and referees, and thank all involved for their patience, intellectual generosity, and constructive comments. We believe that our revision now addresses the effects of collective navigation on the eco-evolutionary dynamics of two populations connected by dispersal, and hope that we have fully addressed the concerns of the referees. We thank the editors for another opportunity to submit a revision to *Philosophical Transactions*, and look forward to further correspondence. Please let us know if any of the below points require additional clarification.

Sincerely,

Justin Yeakel
Jean Philippe Gibert
Thilo Gross
Peter Westley
Jonathan Moore

Comments are in [Blue](#); Responses are in Black

[Editor:](#)

1) Equation 4

We have already been in touch about equation 4. Please follow Reviewer 1’s and Dr. Torney’s guidelines to rederive Lande’s equation using your specific genotype distribution suited to your two-patch system.

0.1) We thank the editor for this observation and acknowledge the error on our part. We have now corrected this, and the equation now mirrors that presented by Ronce and Kirkpatrick. We have written a detailed supplement that explores the problem of tracking the evolution of a mixed trait distribution (Supplementary Information) to 1) describe the inherent complexity (and to justify that an approximation is useful), and 2) to show where and how we make the approximation. Importantly, the approximations and assumptions made in this model are those made in the Ronce and Kirkpatrick model, and they explicitly show that the approximation does not alter the dynamics in a meaningful way.

2) Symmetry

When we discussed this my understanding was that you would address the reviewers' concerns by altering one or more of the site-specific parameters (eg $r_{\max_1} = 2 \cdot r_{\max_2}$, or $\beta_1 = 2 \cdot \beta_2$) and I was surprised when you didn't. I agree that adding symmetric noise, as you have done, is not convincing. Perhaps symmetry isn't driving the results, but let's make sure.

0.2) We think that this was a misunderstanding, and apologize for our lack of clarity. We are confident that symmetry alone is not underpinning our results. We have come to this conclusion as we sampled different values for r_{\max} and β for both populations from a distribution, but held these sampled values constant over time to get the steady state solutions. Sampling was conducted from more variable distributions as the asymmetry parameter increased, and the qualitative dynamics were shown not to change. This shows that the system is relevant across a large asymmetric parameter space, and believe that this was what was asked of us by the referee, though accept responsibility for not clearly communicating our approach. We have simplified the analysis so that $r_{\max_1} = (1+\alpha)r_{\max_2}$, and $\beta_1 = (1+\alpha)\beta_2$, where an increase in α increases the differences between the vital rates between site 1 and 2. The result is the same, though with less variable steady states, as expected.

3) Bifurcation analysis

Once equation 4 has been corrected, or you have verified that the current version is indeed correct, a proper bifurcation analysis is needed. My advice would be to bring in a dynamical systems expert who understands, and perhaps shares, the reviewers concerns and have them advise in that endeavour.

0.3) We thank the editors for their recommendation, and have added a fifth author (Dr. Thilo Gross), who is an expert in dynamical systems. In this new draft, we have endeavored to establish a better understanding of the bifurcation regimes and what they mean for the dynamics of the system. We now have a clear discussion of the bifurcations, and more importantly, how the dynamic regimes that emerge impacts robustness. See response 1.3) for additional detail regarding our understanding of the bifurcations.

4) Refocus

a) Since the fixed dispersal case has (largely) been treated by Ronce and Kirkpatrick (2001), perhaps it would be good to focus more on the density-dependent case. This is most inline with the special issue anyway.

b) You might consider using a simple agent based model, rather than the Lande formulation and focusing more on the questions that I understand originally motivated the paper rather than the more technical aspects (bifurcation taxonomy etc).

0.4) We have completely refocused the manuscript to examine the effects of density-dependent straying by extending the established Ronce and Kirkpatrick eco-evolutionary

dynamic model. Because this model has been studied and shown to be robust against the assumptions that are made, we do not employ an agent-based model, though we agree that this would be a potentially promising future direction to explore some of the more complex relationships.

5) Life history

Reviewer 1 also suggests that equation 4 should reflect the iteroparous life history of your model. This should be done, but it also brings up a more general point. Why are you using a iteroparous model if salmon are the species you have in mind?

0.5) We acknowledge that overlapping generations introduced complexities that our model did not account for. We have eliminated the potential for generations to overlap, so that our revised model is only appropriate for semelparous populations with simple age structure (consistent with Pink salmon life history). We note that not all salmon species are semelparous, and some have life-histories that are quite complex with many overlapping generations due to extensive age structure. We think that this simplification very much aids the focus of the revised submission.

6) Small things

a) Consider changing the title to something like “Eco-evolutionary dynamics density-dependent dispersal: implications for salmon metapopulation robustness”. The ‘collective dispersal’, at least in my opinion, suggests groups of animals collectively deciding to disperse. Also ‘density-dependent’ is more general, potentially connecting your study to more systems.

b) Units would probably be helpful for Table 1. Also instead of var. you could put the range of values used. Evolving quantities can be marked evolvable.

0.6) We have changed our title to: *Eco-evolutionary dynamics, density-dependent dispersal, and collective behavior: implications for salmon metapopulation robustness*. We believe that this better addresses the key themes that are established in this revision.

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Referee: 1

I am unsatisfied with several of the responses by the authors.

Comment/Response 1.1

I maintain that eq. 4 is incorrect, the authors have misunderstood my criticism. As an example, take the case when $w_i \rightarrow 0$ (e.g. $N_i \ll N_j$). Then the derivative in eq. 4 is (nearly) zero, implying no selection on the trait. This limiting situation corresponds to a local population where almost every individual is an immigrant, and in reality, there would be strong selection on these immigrants to adapt to the local optimum.

I notice also another problem with eq. 4. With overlapping generations, it should matter what fraction of the population in $t+1$ consists of new recruits (affected by selection) and what fraction is made of the surviving immigrants (no viability selection acts on the adults). Eq. 4 weighs the change in the mean phenotype as if all individuals were new recruits, in contradiction with eq. 1.

1.1) We thank the referee for describing their concerns and acknowledge that we did misinterpret their initial critique. Thank you for catching the error with Equation 4 in our previous version, which we have now re-derived and note that it is now synonymous with that described by Ronce and Kirkpatrick (Evolution, 2001). We have also provided a detailed supplement that justifies why we employ a Gaussian approximation for the mixed distribution, which is the same approximation that was used by Ronce and Kirkpatrick.

Importantly, we have simplified the model to focus on the case of non-overlapping generations, and now see that our previous equation did not deal correctly with this in any case.

Comment/Response 1.2

In response to the similar model by Ronce and Kirkpatrick (2001), the authors inserted the following sentence in the ms: "This model formulation has parallels to that proposed by Ronce and Kirkpatrick [ref], where habitat specialization evolves between two populations as a function of dispersal, yet differs in that we treat trait evolution mechanistically at some cost to analytical tractability." The criticism to R&K is more explicit in the authors' response to Reviewer II: [in R&K's model] "the strength of selection is determined by the linear difference of trait values and their optima (rather than by mechanistically incorporating the fitness landscape a la Lande 1976)".

Ronce and Kirkpatrick treated trait evolution mechanistically, using Lande 1976: The linear difference of trait values and their optima comes from the derivative of the quadratic selective mortality (the last term in R&K's eq. 1). Next to similarities, there are also important differences between the present results and R&K, the latter found alternative attractors (see more on this below).

1.2) We thank the referee for noticing this, and agree that our revised formulation is nearly identical to that of Ronce and Kirkpatrick (2001). We have reformulated much of the manuscript, and essentially extend their foundational model to explore to what extent density-dependent dispersal alters the dynamics and explore consequences of robustness in the context of environmental disturbance.

Comment/Response 1.3

A) Discrete dynamical systems have pitchfork bifurcations, see for example Richard A. Holmgren: A First Course in Discrete Dynamical Systems, 2nd ed, Springer 1996, p. 62. The fact that an eigenvalue equals +1 is not sufficient to call a fold bifurcation, because non-degeneracy conditions must also be satisfied (see e.g. Kuznetsov's book). A pitchfork bifurcation is the simplest case of eigenvalue=+1 with the non-degeneracy condition of the fold bifurcation violated.

The bifurcation you have is not a cusp. While it is technically correct that traversing a cusp point through a straight line tangent to both fold lines that meet at the cusp results in a pitchfork bifurcation, the important difference is that calling a cusp implies the existence of the two lines of fold bifurcations that meet at the cusp, and you do not have any fold bifurcations at all. Lines 178-182 of the ms are incorrect, they refer to fold bifurcation lines that do not exist in the model.

1.3) We now have a much better picture of the bifurcation regimes in the model, and agree with the referee that what we had interpreted to be a cusp bifurcation was not a discrete cusp

bifurcation. Moreover we acknowledge that the referee was correct in pointing out that there is a pitchfork bifurcation in this system, and thank the referee for pointing out both errors.

In an effort to capture a more complete picture of the bifurcations, we have invited Thilo Gross, an expert in dynamical systems, as a coauthor. The full description of the bifurcation regimes is now explained in the first paragraph of the Results section. To summarize: as straying is increased, the first regime that is encountered has a single symmetric fixed point, and both populations persist at equal population size. A fold bifurcation then occurs in which an asymmetric (low- and high-density) fixed point is created. Initial conditions determine which of the fixed points are approached. The dividing line that separates initial conditions that approach the symmetric solution and initial states that approach the asymmetric solution is a separatrix that runs through an unstable fixed point that was also created in the fold bifurcation. As we increase the straying rate this basin of attraction shrinks and eventually vanishes. At this point the unstable asymmetric state that was created in the fold bifurcation collides with the stable symmetric state. A bifurcation occurs in which the unstable asymmetric state vanishes and the symmetric state is destabilized. This is a subcritical pitchfork bifurcation that only occurs in systems with symmetries. After this bifurcation the stable asymmetric state is the only attractor. After this point, we find a wide regime (regime II) where the system will always approach an asymmetric state where one population is suppressed. However, if the straying is increased further the imbalance in population sizes becomes harder to maintain. As the straying rate is increased we reach a critical point where the stable asymmetric fixed point becomes symmetric and collides with the unstable symmetric fixed point. The system undergoes a bifurcation that is the supercritical form of the subcritical bifurcation encountered earlier. In this bifurcation the stable asymmetric fixed point vanishes while the unstable symmetric state is stabilized. After this bifurcation the symmetric state is the only attractor in the system.

We emphasize that our paper explores the effects of these bifurcations, though we do not include an in-depth mathematical treatment of the conditions, primarily because we think that this will be distracting to the more general points of the paper. Importantly, these are exactly the same dynamic regimes as explored in Ronce and Kirkpatrick, and much of our revised manuscript is focused on examining how these regimes change with density-dependent straying.

B) The hysteresis shown in figure S4 is not explored properly. Do the authors claim to have found more stable equilibria than what is shown in Figure 1; i.e., is Figure 1 incomplete?

The bifurcation shown in Figure 1 may well be a pitchfork bifurcation (cf above and also Reviewer II). But I was somewhat uncertain about this when I wrote the first review, and I am still somewhat uncertain. The two branches separate very quickly, which may indicate that there is an unseen attractor and the algorithm used to draw the figure may be switching to that attractor. The new claim of hysteresis makes the situation only more uncertain. Hysteresis does accompany cusp bifurcations but not pitchfork bifurcations what this model seems to have; the hysteresis comes from the two fold bifurcations associated with the cusp, and the authors have not found any fold bifurcation. The text refers to similar results by R&K, but R&K did find the alternative attractor causing the hysteresis, whereas Figure 1 of the present ms does not show alternative attractors. I agree with Reviewer II that a proper bifurcation analysis needs to be done (using correct equations – see above).

1.4) We thank the referee and now have a much better understand of the dynamics in this system (described in the first paragraph of the Results), aided by our collaboration with Thilo Gross, who is now an author on the paper. We believe that our model presents exactly the same dynamics as R&K, and note that they do report regions of bi-stability, where “both

asymmetric and symmetric equilibria are equally stable", as is described in the caption to Figure 4 of Ronce and Kirkpatrick (2001). Our revised Figure 1 now shows this dynamic as well, which has important consequences for the role of density-dependent straying.

Comment/Response 1.5

The authors' response does not clarify whether the portfolio effect is a useful measure of metapopulation robustness. The ms still introduces the portfolio effect to this end (the definition is given under the heading "Measuring metapopulation robustness" in line 140; the Discussion reiterates this in line 290). I maintain that the portfolio effect is not a good measure of robustness (see my first review), and I do not believe that the metapopulation is particularly safe from extinction near the pitchfork bifurcation as suggested by Fig 2c.

1.5) We agree that the portfolio effect is not always a good descriptor of robustness, and in the revised version of the manuscript, we provide a more nuanced perspective of the risks associated with different levels of straying and strengths of collective behavior. We also discuss cases where the portfolio effect does not seem to be a good indicator of robustness. In addition to the portfolio effect and the time to recovery, we also examine how differences in steady state densities are impacted by straying, and how these measures are in turn altered by the different types of disturbances that are applied to the metapopulation. While imperfect and insufficient on its own, we maintain that the portfolio effect is an important metric because it helps us link the theoretical concepts that we present to the types of measures empiricists collect in wild populations. Generally, while acknowledging the cases that the referee points out, higher portfolio effects do correspond with shorter recovery times (measured as recovery of the aggregate biomass), while lower portfolio effects correspond to longer recovery times (see Figure S3).

Comment/Response 2.2

The scattering cloud of points in figure S13 is not suitable to analyse the bifurcation pattern in asymmetric systems. The authors should produce bifurcation diagrams similar to figure 1 but with parameters fixed for values that differ between the two habitats.

When symmetry is broken, the pitchfork bifurcation should indeed be replaced by a fold bifurcation + a non-bifurcating branch of equilibria. This is what the authors call an "imperfect pitchfork" in their response (but the name is coined here). The fold bifurcation is generic (unlike the pitchfork bifurcation), and gives a much more reliable picture of reality (which is ca never symmetric). In light of this, figure S13, reinforcing the image of a pitchfork bifurcation, is unexpected and requires an explanation rather than itself explaining the behaviour of the system.

1.6) We think that this was a misunderstanding, and apologize for our lack of clarity. Originally, we sampled different values for r_{max} and β for both populations from a distribution, but held these sampled values constant over time to obtain the steady state solutions. Sampling was conducted from more variable distributions as the asymmetry parameter increases, and the qualitative dynamics were shown not to change. This shows that the system is relevant across a large asymmetric parameter space, and believe that this was what was asked of us by the referee, though we did a poor job at conveying this. We have simplified the analysis so that $r_{max_1} = (1+\alpha)r_{max_2}$, and $\beta_1 = (1+\alpha)\beta_2$, where an increase in α increases the differences between the vital rates between site 1 and 2. The result is the same, though with less variable steady states, as expected.

We note that we did not coin the term 'imperfect pitchfork', and point the referee to Strogatz (Nonlinear Dynamics and Chaos, 1994), section 3.6 (Imperfect bifurcations & catastrophes),

which includes discussion of an imperfect pitchfork bifurcation. Again, we no longer believe that this is relevant to our system, but do not wish to assume credit for coining this term.

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Referee: 2

Following the first round of reviewer's comments, the authors have adjusted some elements in the manuscript and responded to the comments in their letter. Here I will comment on some of the changes, the ones which in my view are the most fundamental problems with the analyses presented in this manuscript and to some of the responses from the authors on comments from reviewers. As a general note, several of the mistakes, especially with respect to the bifurcation analysis, potentially render the entire analysis erroneous.

Another general note pertains to the extensive copied-and-pasted explanation of normal forms and bifurcation conditions, taken presumably in part from Kuznetsov's "Elements of Applied Bifurcation Theory, Second Edition". None of the normal forms are derived for the current system under study, which means that typing them out in the response to a reviewer's comment is not very informative. In addition, considering the importance of Kuznetsov's Elements, the authors could also have stayed consistent with the book's formulation throughout the manuscript and referred to 'fixed points' instead of equilibria and 'multipliers' instead of eigenvalues, as applicable for discrete time systems.

2.1) We thank the referee for their constructive review, and admit that there was an error in Eq. 4, which we have since corrected. Our dynamical system is now nearly exactly the same as Ronce and Kirkpatrick 2001, as was noted in the first round of reviews. We have also reformulated the primary aim of the manuscript to focus on to what extent density-dependent straying alters the dynamic regimes that Ronce and Kirkpatrick describe.

To clarify, in our prior response Kuznetsov was cited and not copy-pasted, and our only intent was to use the normal forms that Kuznetsov presents to argue our perspective. We acknowledge our error in interpretation of the bifurcation as a discrete-cusp, and thank the referee for pointing this out. We have a more complete understanding of the bifurcations involved, and point the referee to response 1.3) for details.

We do not think an ecological audience will generally be familiar with the term 'multipliers', and avoid discussing eigenvalues altogether in the revised text.

Separate points

Fig's S4, S9, S10 contain elements that look like artifacts. These are possibly caused by more upload issues, but I cannot assess that. At the same time, since I assume I see the figures as intended, the discontinuous elements, the 'strange' lines (vertical line-elements in fig. S9 for example, the sharp angles in figure S4), should be (have been) looked into thoroughly and analyzed properly.

2.2) We are not sure about the artifacts (possibly an upload issue - we cannot assess this either - it certainly affected one of the figures used in the main text), but we have vastly restricted our analyses to focus our manuscript on density-dependent straying rather than more extraneous analyses. We think that the sharp angles described were issues with the pdf, as they are not present in our figures.

Fig S13 in itself shows that the introduced error or randomness does not resolve the issue with perfect symmetry.

Wherever 'rate' is used in a parameter's or variable's description in Table 1, should that not have been formulated as a fraction, since the manuscript deals with discrete time equations?

It looks like R_i can reach values above 1.0, how does this work and is it not supposed to represent a fraction?

r_{max} - see two comments above

2.3) We think that this was a misunderstanding, and apologize for our lack of clarity. Originally, we sampled different values for r_{max} and β for both populations from a distribution, but held these sampled values constant over time to obtain the steady state solutions. Sampling was conducted from more variable distributions as the asymmetry parameter increases, and the qualitative dynamics were shown not to change. This shows that the system is relevant across a large asymmetric parameter space, and believe that this was what was asked of us by the referee, though we did a poor job at conveying this. We have simplified the analysis so that $r_{max_1} = (1+\alpha)r_{max_2}$, and $\beta_1 = (1+\alpha)\beta_2$, where an increase in α increases the differences between the vital rates between site 1 and 2. The result is the same, though with less variable steady states, as expected.

Comments in response to specific responses

Response 1.3

The discussion of the Discrete Cusp Bifurcation does not make any sense to me. Cusp bifurcations are codimension 2 bifurcations (meaning occur under fulfillment of two, independent, parameter conditions), and hence would show up in bifurcation analyses of two parameters. The potential occasion that a Cusp bifurcation would be encountered while following a codim-1 curve, would not be possible to visualize as fig. 1 in the manuscript. See the attached png (9.2) from Kuznetsov 1998 as illustration.

More comments in response to exact wording:

"Our understanding is that the fold bifurcation is a general attribute based on this eigenvalue condition, but as the Reviewers indicate, it is not a particularly clear or complete description of what is going on."

I disagree, the identification was incorrect, not unclear nor incomplete. The new identification is incorrect also.

"A familiar, and more complicated bifurcation that occurs in maps with ≥ 2 parameters is the Discrete Cusp Bifurcation, which occurs when two fold bifurcations intersect at a cusp."

This is an incorrect interpretation of the codimensionality of 2 for Cusp bifurcations (including those occurring in discrete-time systems). As explained above, a Cusp bifurcation has codimension 2. This is defined by Kuznetsov (1998) as:

'We introduce the notion of codimension (codim for short) in a rather naive way as the number of conditions defining the bifurcation.'

The current analyses does not go into 2-parameter analyses anywhere. In case a Cusp bifurcation would be encountered in an analysis of one parameter, it would be impossible to show the dynamics as occurring in fig. 1 (see below for more details).

"A one-dimensional transect through the cusp results in behavior similar to that observed for Pitchfork Bifurcations in vector fields (topological normal form for the discrete map: $x \rightarrow x + \beta x - x^3$)."

This concerns a scenario where two bifurcation parameters are exactly such that the system's solution is 'at' the Cusp bifurcation. Firstly, in this scenario the bifurcation graph would show an S-shaped relation of the population fixed-point density with the bifurcation parameter, not anything like what occurs in fig. 1. Secondly, reporting only the dynamics at an alleged Cusp bifurcation point would be an omission of the wider (biologically relevant) parameter space. But as said, I do not believe this is what is illustrated in Fig 1.

"We now identify the bifurcation as a Discrete Cusp bifurcation and mention that it displays dynamics that are visually similar to Pitchfork bifurcations in continuous time systems, which we hope will increase clarity and specificity."

This is incorrect and moreover shows that a proper system analysis is required before conclusions can be drawn with respect to the system dynamics and implications for ecological systems.

2.4) We now have a much better picture of the bifurcation regimes in the model, and agree with the referee that what we had interpreted to be a cusp bifurcation was not a discrete cusp bifurcation. Moreover we acknowledge that the referee was correct in pointing out that there is a pitchfork bifurcation in this system, and thank the referee for pointing out both errors. We have a more complete understanding of the bifurcations involved, and point the referee to response 1.3) for details.

Response 2.2

I understand that the dynamics of a system that deviates from perfect symmetry may still resemble Pitchfork bifurcation-like equilibrium dynamics. I disagree that this points towards the author's having analyzed a system including appropriate asymmetry.

Specifically:

".. the system is asymmetric, however the pitchfork-like dynamic does not disappear but becomes an imperfect pitchfork where a saddle node bifurcation appears alongside a non-varying steady-state. This creates a parameter region where alternative steady-states exist, separated by an unstable steady-state. "

It would be good if the dynamics described in the quote above were also shown for the system under study.

The further response makes me wonder why the authors did not use their analytical results to derive what exactly are the bifurcation parameters.

The introduced randomness using Normal distributions with the same parameters does not do much towards 'breaking symmetry'.

2.5) With regard to the above concerns, please refer to response 2.3, which clarifies our examination of asymmetrical vital rates. Importantly, increasingly asymmetric vital rates do not affect the primary dynamic that we explore in the model - that of asymmetric (high/low density) stable states. As we are concerned primarily with the biological implications of this dynamic, rather than a complete and formal mathematical treatment, we contend that we have shown that the model formulation - though it certainly contains symmetries that are hardwired, which lead to the bifurcations observed — applies to populations that are linked by dispersal but do not have identical vital rates. For the problem that we examine here, we believe that this is

the relevant question to address, and hope that our revised explanation and simplified analysis is satisfactory.