

25 November 2019

Dear Dr. Alyssa Findlay:

We are here submitting a revised version of our manuscript “Trophic phenological mismatch: Disconnects between underlying ecological theory and climate change responses”for consideration as a Review Article in *Nature Climate Change*. We thank the three reviewers for their insightful and constructive comments that have helped make this a much stronger paper. A detailed account of our responses can be found below.

The first two reviewers found our manuscript gave constructive ways forward for the field and provided a useful structuring framework. Reviewer #3, however, had some concerns with our interpretation of the Cushing hypothesis. We regret this assessment and believe it is because we did not make our intentions clear. We have now edited the text to clarify the interpretation of the hypothesis more effectively (lines 114-116; lines 845-879) and re-organized Figure 1. In response to the constructive comment from Reviewer #1, we expand our framework and include a short discussion (lines 447-457) to include those systems that do not meet the criteria for being suitable to test the Cushing hypothesis. Additionally, we have shortened the abstract and main body of the review, as well as dedicated a Box to describe the Cushing hypothesis, and a Box to describe the benefits of integrating experimental and observational approaches.

We believe our paper will be a major step forward in a field that is currently struggling to predict the consequences of climate change-driven shifts in phenological synchrony. By reviewing the state of the literature and putting forward a conceptual framework, we show how advances could come from direct tests of the widely-cited Cushing match-mismatch hypothesis and clear definitions when possible. We hope you and the reviewers will find it suitable for publication. We believe this paper contributes novel and exciting ideas to the fields of ecology and climate change biology. We look forward to hearing your assessment.

Sincerely,



Heather Kharouba (First author)

Reviewer Comments:   
  
**Reviewer #1 (Remarks to the Author):**  
  
I have read the ms ” Trophic phenological mismatch: Disconnects between underlying ecological theory and climate change responses” by Kharouba and Wolkowich.   
  
The ms reviews empirical tests of the match-mismatch hypothesis by Cushing, which underpins much current research on fitness effects of climate-driven phenological shifts. By analysing how the Cushing hypothesis has been dealt with, the authors points out two weaknesses with current studies (failure to collect the appropriate data and failure to define pre-climate change baselines). Based on this, the ms suggests many concrete ways forward to progress on this issue, including a practical framework to guide empirical studies in this area.  
  
I have reviewed a previous version of this manuscript submitted for another journal, and noticed that several issues raised by the different referees in the previous version has been addressed. I will therefore only raise relatively few specific points.  
  
I find the ms overall interesting and the authors makes a serious attempt to provide a better foundation for tests the Cushing match-mismatch hypothesis. This hypothesis is key in much research on phenological shifts and, as shown here, not so well understood as one would expect given the amount of research implicitly or explicitly revolving around it. If it would be possible for the scientific community to relate this theory better to data, it might lead to important breakthroughs. This article and the framework suggested here may help to focus the minds of many researchers. As it is now, theoretical and empirical research in this field are not very well connected, perhaps because it is a young field and many studies has focused on the mere detection of phenological mismatches. But at the end of the day scientific progress requires proper testing of theory.  
  
The ms is overall well written and makes many good points, not least by highlighting the differences in which different empirical studies with regards to generation times, and what the Cushing curve represents (with major differences between terrestrial and aquatic systems). The manuscript also suggests a number of concrete ways to improve tests.

***\* Our response:*** *We thank the reviewer for their kind comments about our framework and our suggestions for moving this field forward. We hope the changes that we made to the manuscript (outlined below) make it even stronger. Please note that the main text has been shortened and we have created two additional boxes in part due to word limits.*

Abstract:  
The abstract highlights problems with current approaches but many researchers are already aware of the shortcomings of their approaches. That is due to trade-offs: we all want to uncover general principles and do strong tests, but that comes with a cost either in terms of time, resources or money. So no-one is surprised by weaknesses in current approaches. It would hence be better to also summarize the specific solutions suggested here. That is the novelty here (problems in phenological research are often pointed out and widely acknowledged).

***\* Our response:*** *We thank the reviewer for their suggestion to make the abstract stronger. We have now prioritized summarizing some specific solutions (e.g., experiments that clearly link timing to fitness and test extremes, integration across approaches, and null models) on lines 49-51 and removed other points in order to shorten the abstract.*

The framework:  
A main novelty of the paper is the framework (Figure 3) which seems very useful to help to discriminate between systems which are suitable vs unsuitable to study the Cushing system. A problem however is what happens in all those cases where the strict criteria are not met. Even if those study systems cannot be used to test Cushings hypothesis, there may at least in some cases exist some adjusted theory/hypothesis which could work as a basis for useful and interesting empirical tests with bearing on ecological consequences of phenological shifts. I think at least this should be discussed somewhere, not least to not disqualify study systems which may be interesting and which people have studied for a long time.

***\* Our response:*** *We thank the reviewer for this helpful suggestion to improve our framework. We believe the reviewer is referring to Figure 2 instead of Figure 3. Consequently, we have added an additional box to Figure 2 and added a section in the main text on lines 529-538 that highlights additional hypotheses that could be tested in systems not suitable to study the Cushing hypothesis.*

Minor comments:  
  
L140 likely->unlikely?

***\* Our response:*** *We thank the reviewer for catching this*. *After further reflection and* *in response to another reviewer’s* *comments, we now clarify that we are discussing total fitness in this review (line 958-959). Consequently, we state that tradeoffs between fitness components are likely (line 958-960).*  
  
L153 introduce ->analyse?

***\* Our response:*** *We have now re-organized this section and had to shorten the manuscript so this phrase is no longer in the paper.*  
  
The figures, especially Fig. 1 and Fig. 3 are not so pleasing for the eye. I think they could easily be made more interesting and informative.

***\* Our response:*** *We thank the reviewer for this constructive feedback to improve our figures. All three figures have been updated and re-worked to make them more pleasing and informative.*   
  
  
With regards to Nature’s criteria for publication I find that:  
Evidence for conclusions: The conclusions of the ms is supported by relative strong evidence: a state-of-the-art literature review + additional relevant literature.   
Novelty: The novelty of the manuscript lies in the practical framework suggested to better bring together the Cushing mismatch theory and empirical data. A weakness of the framework however is that it disqualifies many study systems (see remark above) without discussing those cases much further.  
Importance for the field: as the authors argue, there is a disconnect, and bridging between empirical and theoretical work is important.  
Interest to related disciplinces: phenological shifts is already a cross-cutting theme, and frameworks bridging between theory and empirical tests is needed in other areas as well, including in various effects of climate change such as range shifts and invasive species.  
  
***\* Our response:*** *We thank the reviewer for pointing out the novelty of our paper. We have worked to address**what to do with systems that are not suitable for applying the Cushing hypothesis by adding another box to Figure 2 and an additional section in the main text (lines 529-538).*

**Reviewer #2 (Remarks to the Author):**  
  
In this review, the authors assess the state of the current empirical literature on trophic phenological mismatch. They use a structured review to inform this view, and identify two key assumptions that underlie climate change phenology studies – two assumptions that are frequently violated. Finally, they offer some constructive ways forward to more rigorously investigate the effect of climate change on phenology  
  
I found this to be a well-written, compelling, and comprehensive manuscript. I have very few suggestions for edits. I found the thorough delve into the assumptions of phenology studies to be particularly strong. I feel that this is a strong addition to the literature and should act as a baseline for future empirical work on this subject.  
  
My only major comment is quite minor. However, I found the introduction to the manuscript too broad, particularly between lines ~70-87. Phrases like “general framework” (line 75) and “underlying…theory” (line 81-82) were too vague, and gave the impression that this manuscript addresses a general theory. However, the focus is quite specific (the Cushing match-mismatch hypothesis), though the use of this hypothesis is pervasive. The language should be tightened up to be more specific about the goals of this manuscript and the critiques of the literature.

***\* Our response:*** *We thank the reviewer for helping us improve our writing. This is a good point and one also made by another reviewer. As such, we have: i) made the two paragraphs more specific (lines 73-87); ii) eliminated some redundancies; iii) gotten rid of vague language. Please note that the main text has been shortened and we have created two additional boxes in part due to word limits.*

I have a few further comments by line number below:  
  
Line 82: I’m not sure “attribute” is the right word here, because the authors don’t specify what they are attributing variation TO.

***\* Our response:*** *In the shortening of the main text, this sentence no longer exists.*

Line 150: I don’t agree that these are “theoretical areas”, just two major assumptions that underlie the hypothesis.

***\* Our response:*** *We agree that these are not ‘theoretical areas’ and have removed ‘theoretical’ and leave it as ‘areas’ (line 98).*

Lines 150-153: It would help to number these two “areas” using the same numbering system used in paragraphs below (e.g., “i", “ii”)

***\* Our response:*** *We have now numbered these two areas (lines 100-105).*

Line 158: I would define “performance” here in the main text. It is only briefly defined in the appendix as “growth or development”, but that is useful information that belongs in the main text.

***\* Our response:*** *We have now added ‘growth and development’ as examples of performance on line 109.*

Line 176: “…outcomes of species’ responses to changes” is a vague and confusing phrase when contrasted with the earlier “relationships between organisms and the abiotic environment”.

***\* Our response:*** *Thanks for pointing out this ambiguity. In shortening the manuscript, this sentence no longer exists.*  
  
  
  
**Reviewer #3 (Remarks to the Author):**  
  
Dear Authors,  
  
Your manuscript focuses on the ‘Cushing hypothesis’ in the context of climate change. Unfortunately, I think there is one basic misconception and simplification related to this hypothesis. First, Cushing was not referring to individual fitness as a consequence of resource match/mismatch but to annual stock recruitment in fish, a measure of population mean fitness (please see also specific and detailed comment below). Consequently, the manuscript somehow does not address what it claims to address but simply focuses on individual fitness consequences of match/mismatch.

***\* Our response:*** *We thank the reviewer for raising this concern, as our intention was not to focus solely on individual-level fitness, though we can see now how this was not clear. To address this, we have changed the manuscript in several places. We have clarified on lines 937-938 that Cushing was referring to annual stock recruitment in fish, a population measure of fitness. We also clarify that the Cushing curve represented in Figure 1 is at the population level and refer to population-level fitness changes on line 93. Additionally, we clarify that per-capita estimates of fitness underlie the necessary population-level metric of fitness that the Cushing hypothesis is based on (lines 186-187) and that individual-level data is needed to understand population-level connections between timing and fitness of the consumer (lines 218-219).*

Second, you simplify the ‘Cushing hypothesis’ to an extent that makes testing it problematical: If do you not find a study you reviewed in agreement with the hypothesis, it could be (1) because the hypothesis genuinely does not apply here or (2) because other mechanisms that were omitted when simplifying the hypothesis are important. For example, if you found a seasonal decline in fitness, rather than the expected hump-shaped curve peaking at maximum resource abundance, it could be because a seasonal fitness decline caused by priority effects in a migratory species ‘overrules’ the fitness consequence of relative timing to the resource.

***\* Our response:*** *We thank the reviewer for raising this related concern, as this was not our intention, though we can see now how our aim was not clear. To address this, we have changed the manuscript in several places. First, we agree that Cushing was talking about population level fitness and clarify that on lines 92, 849-850. Second, given the complexity of the hypothesis, we aimed to simplify it by not focusing on total fitness. However, after reading the reviewer’s concerns, we agree this is too narrow and now explicitly consider total fitness. We now clarify on lines 903-906 that we consider fitness to be total fitness, whether it be lifetime or population-level. We also clarify that we mean total fitness in the caption of Figure 3. Third, as our aim was to simplify the discussion around the hypothesis, we focus solely on the biotic factors that influence fitness, in keeping with the first assumption of the hypothesis. As such, we include this objective and are explicit in the fact that we are discussing the Cushing hypothesis in a narrower context on lines 873-877. As a similar point was also made by another reviewer, we now add a discussion about the usefulness of systems where the Cushing hypothesis does not apply but where alternate hypotheses can be tested (lines 447-457).*

Specific points:  
  
L58-63: Here you jump repeatedly from phenological changes to fitness consequences (resulting from these). It would be easier to read if you deal with one first and then with the other.

***\*Our response:*** *We thank the reviewer for pointing out this lack of organization. To aid in the readability of this first paragraph, we get rid of the* *2nd sentence that specifically discusses the consequences of phenological shifts which is less related to the topic of this paper.*  
  
L64-65: Fitness consequences and phenological mismatch are not the same, or rather only if you define them to be. However, in Box 1 you explicitly state that “Importantly, this term [phenological mismatch] does not incorporate fitness consequences for either species.” Since both terms and their respective meanings are key concepts of crucial importance to your manuscript, I really wonder about this discrepancy.

***\*Our response:*** *We thank the reviewer for pointing out this confusion. We have now clarified the sentence (line 58-59) so that it matches our definition in the glossary. We have defined them as: synchrony- the phenological differences between pair-wise interacting species and does not include fitness consequences. Comparatively, phenological mismatch refers to decreases in consumer fitness associated with changes in the relative timing of life cycle events. Thus, we believe the reviewer is quoting our definition of ‘phenological synchrony’. Nonetheless, we can see that we should have been clearer and thus have adjusted the text. We are also explicit that*

*we follow the connections between mismatch and fitness which follows other studies (lines 966-967).*  
  
L68-70: These sentence is very vague. Almost to the extent that it becomes meaningless. What do you exactly mean by “have worked to improve predictions and address diverse findings”?

***\*Our response:*** *This is a good point and one also made by another reviewer. We have removed ‘address diverse findings’ and made the sentence more specific (line 65-66). Please note that the main text has been shortened and we have created two additional boxes in part due to word limits. The introduction has been trimmed and clarified throughout (further detailed throughout our response).*  
  
L77-87: This paragraph is generally fairly vague. I agree that “a disconnect between ecological theory and current empirical approaches” may exists and hamper our predictions about future climate change-induced mismatches but at this part of the manuscript it should have become more specific what the problems are.

*\*Our response: We thank the reviewer for pointing out our lack of clear writing in this section. We have now re-worked it (lines 75-89) to be more specific.*

L108-110: Having read some of the papers cited here (Cushing 1969, 1990), I doubt that the widely used concept of the hump-shaped relationship between (relative) consumer timing and its fitness was introduced by Cushing. In none of the cited papers a fitness-timing relationship is shown. Fig.2 in Cushing (1990) shows frequency distributions of eggs, larvae and larvae food, which are depicted hump-shaped, but not fitness against timing. The match/mismatch hypothesis laid out in these papers concerns the match between (relative) timing of fish larvae and their (planktonic) food but the consequences in that Cushing was interested was not individual fitness but annual stock recruitment, which is a component of population mean fitness.

***\*Our response:*** *We thank the reviewer for highlighting this confusion. We agree that the consequences of mismatch are not directly shown in Figure 2 of Cushing (1990). However, we feel, along with other studies (e.g., Durant et al. 2007, Johansson et al. 2015, Visser and Gienapp 2019), that this is a prediction of the hypothesis if you assume that match has the highest fitness. We have reworked the section (now Box 2; 933-970) and Figure 1 to make this clearer. We now introduce Cushing’s hypothesis first (lines 933-941) and then expand the hypothesis to include the assumption we are making about match meaning the highest fitness (lines 942-944), and the resulting prediction (lines 944-947).*

L114-116: I do not think that ‘life-history theory’ predicts necessarily a match between consumer demands and resource availability. It could rather be the explanation for an ‘adaptive mismatch’ if trade-offs between resource matching and a general seasonal fitness decline (or increase) lead to the ‘total fitness’ optimum being shifted away from the resource peak (e.g. Johansson & Jonzén 2012, Am Nat 179:463-474; Johansson et al. 2015, Oikos 124:102-112).

***\*Our response:*** *We thank the author for this and have removed the reference to life history theory in this section (lines 850-851). We have also added text on lines 116-119 to be explicit that tradeoffs could also shift the fitness optimum away from the resource peak (i.e. the adaptive mismatch hypothesis).*  
  
L117-119: This is a more minor point but I think a clean terminology is important, especially when presenting an ‘overview over the main ecological theory’. Selection is a population-level phenomenon as what matters for selection is the fitness of a phenotype relative to the fitness of all other phenotypes present in the population. In a population with no variation in phenotypes no selection will be present, even if this phenotype is far removed from the optimum. What you describe here, however, is simple the shape of a fitness function and the fact that individual absolute fitness will drop if an individual’s phenotype ‘moves away’ from the optimum.

***\*Our response:*** *We thank the reviewer for pointing out this ambiguity. As in the response to the previous comment, we removed the mention of selection here and adjusted the text to be more clear (lines 942-947).*

L132-140: If I understand you correctly, here you assume individual fitness is highest ‘at match’ (for the ‘focal species’, the consumer). This simplification can, however, be misleading, especially when planning to scrutinize evidence for the match/mismatch hypothesis. For example, if a study finds that individual fitness does not peak ‘at match’, this could be because there are other fitness components that are unrelated to synchrony with the resource, have a maximum at a different time and hence shift the ‘total’ fitness optimum away from match (see also point raised above).

***\*Our response:*** *We thank the reviewer for raising this concern, as our intention was not to overly simplify this hypothesis. We agree that being clear about which measure of fitness we are using and the assumptions we are making is crucial. To address this, we have changed the manuscript in several places. First, we now clarify that we mean total fitness and include either lifetime or population mean fitness (lines 871-872). Second, we clarify that, consequently, this could mean that tradeoffs are possible (lines 873), and could lead to a match or mismatch (lines 114-119). Third, we clarify that a detection of ‘match’ could also depend on which fitness components have been measured in the study (e.g., reproductive success vs. lifetime fitness), discussed on lines 375-376.*

L148-154: It seems you here lay out the aim objective of your study and your literature review. It is, however, not made very clear what exactly the issues are. If studies ‘fail to rigorously test the Cushing hypothesis’, this could very well be due to ‘data limitations’, which you, however, state above is not the focus of your study. It has not yet become clear why testing ‘pre-climate change conditions’ is relevant, either. Being already this far into the Introduction the main aim of your study should have become clear because otherwise you risk to lose the interest of the reader. I would have definitely laid your paper aside at this point if I did not have to review it.

***\*Our response:*** *We thank the reviewer for pointing out the lack of clear language in this section. We now outline and expand on the two main issues on lines 143-149, as well as removed the point about dismissing data limitations as something we are not discussing.*

L155-158: If not already done, I would have definitely expected that the ‘two key theoretical areas’ (L150) that you aimed to address would have been explained here in sufficient detail. Instead you start with classifying the reviewed literature.  
  
***\*Our response:*** *This is a good point and, and we now expand on the two main issues on lines 143-149.*

L161-163: Without having read all the reviewed papers I cannot be sure, of course, but I doubt that these studies really aimed at predicting impacts on ‘ecological communities’. Rather I assume that these studies mostly focused on one consumer species and its food because of the complexity of species communities.

***\*Our response:*** *Good point,**we have changed ‘ecological communities’ to ‘pair-wise species interactions’ on lines X.*  
  
L175-177: What would be the difference between “direct relationships between organisms and the abiotic environment” and “species’ responses to changes in abiotic factors” that you allude here to?

***\*Our response:*** *We thank the reviewer for pointing out this ambiguity. We have now clarified this sentence on line 183-188.*  
  
L178-179: I really find “testing the assumptions and ultimate mechanisms from a diversity of ecological and evolutionary theory” very vague.

***\*Our response:*** *Agreed,**we have now removed ‘from a diversity of ecological and evolutionary theory’* *on lines 174-175*.

L184-187: I do not agree with this. As I laid out above already more than once, trade-offs between fitness components are likely to move the fitness optimum away from the resource peak and/or lead to different asymmetric shape of the ‘Cushing curve’.

***\*Our response:*** *We thank the reviewer for pointing this out. We now clarify that tradeoffs between fitness components are possible (lines 873), and could lead to a mismatch with the resource peak (lines 114-119). We also remove the phrase ‘this forms the theoretical basis for the original hypothesis’ on line 116-117.*

Furthermore, I think it needs some explanation how bet-hedging alone can lead to a hump-shaped fitness function as this is not directly evident.

***\*Our response:*** *Agreed,**we have now added a discussion of alternative hypotheses, which includes the bet-hedging hypothesis (lines 447-457).*  
  
L196-199: Here it seems you equate ‘density dependence’ or ‘top-down population regulation’ with a ‘life-history trade-off’, which I find very surprising.

***\*Our response:*** *We do not mean to equate those two mechanisms with a life history tradeoff. We think the confusion was related to the reference to life history tradeoff in the first sentence of the paragraph (lines 197-198) so we have now removed it.*  
  
L199-200: Unfortunately, it is unclear here what the mentioned ‘assumptions’ exactly are.

***\*Our response:*** *We clarify the assumptions by adding an “i.e.” on line 129-130.*  
  
L203-206: What ‘diversity’ exactly do you mean?

***\*Our response:*** *Good point, we clarify our meaning on line 132-133 as “the number of mechanisms. We also changed our use of “diversity of ecological theory” on line 149 to the “several mechanisms”.*  
  
L216-218: It is likely very true what you write here but I do not see how this would linked to the ‘Cushing hypothesis’ discussed here.

***\*Our response:*** *Thanks for pointing this out****. W****e have clarified our language on lines 145-146 to relate specifically to the meeting of the first assumption.*  
  
L226-227: As pointed out above, selection is a population-level phenomenon. Please be more accurate with the terminology.

***\*Our response:*** *We thank the reviewer for highlighting our inaccurate language. We have now gotten rid of the reference to selection (lines 157-158).*

L227-203: Why this would be the case is not immediately clear and would require further explanations.

***\*Our response:*** *We have added a more detailed explanation on lines 237-238.*  
  
L231: That a test of a hypothesis requires testing the underlying assumptions is obvious and redundant.

***\*Our response:*** *To reduce redundancy, we have removed the phrase ‘clear tests of the assumptions’ on line 227.*

References:

Durant, J. M., Hjermann, D. Ø., Ottersen, G. and Stenseth, N. C. Climate and the match or mismatch between predator requirements and resource availability. *Climate Res.* **33**, 271-283 (2007).

Johansson, J., Kristensen, N. P., Nilsson, J.-Å. and Jonzén, N. The eco-evolutionary consequences of interspecific phenological asynchrony--a theoretical perspective. *Oikos* **124**, 102-112 (2015).

Visser, M. E., and Gienapp, P. Evolutionary and demographic consequences of phenological mismatches. *Nature ecology & evolution* **3**, 879-88 (2019).