**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 these we have changed the manuscript in several places. First, we have clarified on lines 103-105 and lines 126-128 that Cushing was referring to annual stock recruitment in fish, a population measure of fitness. We also clarify that the Cushing curve is at the population level (line 128; also need to add to caption of Figure 1). Second,*

*our aim was to discuss both individual metrics that make up the relevant population-level processes and we hope our revisions to the manuscript have made this more clear. We do note that individual-level measures of fitness are needed to provide strong tests of the hypothesis since there are several potential mechanisms underlying the Cushing hypothesis, which we discuss on lines 232-233.*

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 our intention was not to simplify this hypothesis to such as extent it would make it irrelevant, though we can see now how our aim was not clear. Our aim was to focus on the biotic factors influencing fitness, which is in line with the first assumption, and consequently our discussion of the hypothesis is more narrow. We do realize this discussion is more narrow than other studies (Visser and Gienapp 2019).*

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 63-64) 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 more clear and thus have adjusted the text.*

*We feel, along with other studies (e.g. Miller-Rushing et al. 2010, Johansson et al. 2015,* *Visser and Giennap 2019), that the distinction is crucial, as not all studies have quantified the fitness consequences of shifts in the timing of species interactions. We follow the connections between mismatch and fitness which is in line with numerous other studies (check Durant ).*  
  
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:*** *We have removed ‘address diverse findings’ and made the sentence more specific.*  
  
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 have now re-worked this section (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, that this is a prediction of the hypothesis if you assume that match has the highest fitness. We have reworked the section (lines 100-118) and Figure 1 to make this clearer. We now introduce Cushing’s hypothesis first and then expand the hypothesis to include the assumption about match meaning the highest fitness, and the resulting prediction.*

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 their perspective and have removed the reference to life history theory in this section. This overview of the hypothesis now matches the definition in the Glossary and caption of Figure 1. We agree that adaptive mismatch could be another explanation and discuss this mechanism on lines X.*  
  
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 author for pointing out this ambiguity. As in the response to the previous comment, we removed the mention of selection here.*

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 pointing out this confusion. We agree that being clear about which measure of fitness we are using is crucial. We have now clarified on lines 127-129. While we agree that Cushing was referring to a population measure of fitness and that the curve is at the population level, we do not assume that peak fitness in this context is the same as total fitness. Instead, we consider fitness as a single component (lines 128-131). As a result, trade-offs between components are likely. We note that with a broader definition of fitness, such as population mean fitness, the first assumption of the Cushing hypothesis would not be met (i.e. that the resource is a the major controller of consumer fitness).*

*We agree that with our definition of fitness, it is possible the fitness optimum may not be a ‘match’. It is also possible that a detection of match vs. mismatch could depend on which fitness components have been measured in the study (e.g., reproductive success vs. lifetime fitness), discussed on lines 375-376.*

*Finally, we note that selection and population demography are both affected by individual variation in survival and reproductive success. Therefore, understanding the links between individual fitness, natural selection and population demography is key to stronger tests of this hypothesis.*

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 get rid 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:*** *We have changed ‘ecological communities’ to ‘pair-wise species interactions’*  
  
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:*** *Thanks for pointing out this ambiguity. The distinction between the two phrases is the word outcome. 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 agree that trade-offs between fitness components could lead to no peak or a different shape of the Cushing curve. However, this end result depends on which component of fitness is ultimately favoured. To be more consistent that multiple mechanisms could underlie the Cushing hypothesis, we remove the phrase ‘this forms the theoretical basis for the original hypothesis’ on line 197.*

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:*** *We have added an example line 192-194 to help readers better understand bet-hedging as a mechanism in this context. Specifically, that species that use bet-hedging are unlikely to meet first assumption of hypothesis.*  
  
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 thank the reviewer for pointing out this confusion. 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 296-297.*  
  
L203-206: What ‘diversity’ exactly do you mean?

***\*Our response:*** *By diversity we mean the fact that there are multiple mechanisms related to the Cushing hypothesis. We clarify our meaning on line 299.*  
  
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:*** *We have clarified our language on lines 233-234 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 changed the phrase to ‘fitness consequences at the level of the individual level’ on line 328.*

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.*