**Reply to reviewers**

**# Reviewer 1**  
EVALUATION  
Please list your revision requests for the authors and provide your detailed comments, including highlighting limitations and strengths of the study and evaluating the validity of the results, and data interpretation. If you have additional comments based on Q2 and Q3 you can add them as well.  
1. Highlighting limitations and strengths of the study   
Authors used a novel mechanistic approach to infer size-based functional response to make explicit consideration of the movement of organisms in aquatic and terrestrial systems.   
However, the manuscript format is very casual and does not meet the basic requirements of this Journal. And the lack of some necessary elements of academic papers，and different elements are mixed up and confusing.

*The present article is a perspective paper. Thus, its goal is to promote a novel research avenue to investigate the functional response by including factors from the physical medium. The model presented is an example of what can be done. And the discussion of the results points out the strength but also some weaknesses and potential improvements. This is why the format is not the one of a classical research paper.*

2. Evaluating the validity of the results  
The authors propose new models for some existing problems raised by the research in the field, but the authors do not substantially verify the effectiveness of the model.  
The authors did not adopt a classical authoritative approach to verify the effectiveness of the model, for example, using statistical method degrees to validate the degree of compliance between predicted and actual values.

3. Data interpretation.  
The authors did not describe the results.

Detailed comments:  
Abstract:   
What is the aim of this work? What are the main results and conclusions of this work? I suggest that this information should be explicitly provided in the abstract section.  
  
Introduction:  
What are the specific scientific problems proposed to solve in this work?  
What is the relationship in the following parts? For example, line 33 (Introduction), line 65 (Physical features of the medium and size-related constraints), line 129 (A case study as an example of new mechanistic approaches).

*Since it is a perspective article and not a classical research article, the format is different. As we explained above, the goal is to emphasize the need to include factors from the physical medium. The section “Physical features of the medium and size-related constraints” provides a literature review in order to point out the effects of the physical medium on species motion and interactions. The section “A case study as an example of new mechanistic approaches” is an illustration of the kind of model that can be build within this realm. The goal of the paper is not to fully present the model per se.*  
Line117-124. The “novelty” and the “strength” related to the “approach” proposed by the authors, are the highlights of this work, and the author elaborated it is unpredictable, and it is necessary to elaborate in detail.  
  
A case study as an example of new mechanistic approaches  
What does this part do? What's the relationship with “Main framework”? Is the main framework affiliated with the author or the "case study"?

*The case study proposes an example of the kind of model that can be provided following the approach described before. The main framework is the description of the model itself. We agree that this term was misleading. Thus, we replaced “Main framework” by “Case study: derivation of a functional response from size-related mechanical constraints” to make it clearer.*

The confusion arises follows:   
Are the equations (model) from 1 to 4 proposed by the authors or the "case study"?  
What is the foundation for proposing these models?

*Following our response to the former comment, it should be clearer now that the equations are the model proposed as a case study. The foundation of the model is the Portalier et al. (2019) article that considers mechanical factors and body size in a predator-prey interaction.*  
Validation of the model  
How to verify the effectiveness of the model? Are there some specific statistical methods to test the agreement between predicted and actual observations?

Discussion   
Discussions should be an important part of research papers. In terms of this work, it is necessary for the authors to discuss the ecological significance of the established model and its application value deeply.

*Since it is a perspective paper, the aim of the paper is not to promote this model in particular, but to point out what insights can be provided by this kind of approach.*

Animal size is affected by developmental stages as well as contaminants. How will these factors be taken into account in building the models? What are the use scope and limitations of this model? These issues are necessary to be fully discussed.  
However, this manuscript does not contain this part.

*The model considers size. Thus, two individuals taken at two different development stages (for example) would behave differently according to the model. On the other hand, two individuals of the same size would be considered as similar.*

Conclusions  
The conclusion part should be a concise summary of the experimental results, rather than to discuss.

*Since this article is a perspective paper, the goal is not to discuss the experimental results per se, but to promote a novel approach that the model illustrates.*

**# Reviewer 2**EVALUATION  
Please list your revision requests for the authors and provide your detailed comments, including highlighting limitations and strengths of the study and evaluating the validity of the results, and data interpretation. If you have additional comments based on Q2 and Q3 you can add them as well.  
General Evaluation:  
Main findings of the manuscript  
The authors aim to improve our understanding of the predator-prey relationship by including an explicit consideration of the movement of the organisms involved, and hence of mechanics. They provide a model that derives classical parameters of a functional response from body size or organisms involved and physical factors of the medium, which can be easily measured. The novelty is that parameters are not estimated from observational predation data.  
  
Limitations:   
Some wording could be changed for clarity and brevity. In addition, the authors need to provide quantitative data on the model fits, and need to better highlight the novelty of the study.   
  
Strengths:  
Provision of a model that derives classical parameters of a functional response from the easily measured parameters body size and physical factors. Use of the model means that the parameters so not need to be estimated from observational predation data.  
  
Specific Evaluation:  
Title:  
1) Line 1: Can “biomechanical” be changed to something more informative? Line 100 talks about physical properties, which seems like it should be in the title.

We changed the title accordingly. The title is now: “Inferring size-based functional response in aquatic and terrestrial systems from the physical properties of the medium”.

Introduction:  
2) Lines 52-58: Has this relationship of the FR to size already been well established? Need to focus on the novelty of this study.

*We edited the paragraph accordingly (lines 57-59). We explained that our understanding of this well-known relationship would be improved by incorporating the physical medium in models.*

3) Lines 55-58: Could add more references from the marine realm in addition to Williams et al., such as Miller, T. J., Crowder, L. B., Rice, J. A., & Binkowski, F. P. (1992). Body size and the ontogeny of the functional response in fishes. Canadian Journal of Fisheries and Aquatic Sciences, 49(4), 805-812.

*We added the corresponding reference.*

4) Lines 85-88: Seems like body size VERSUS viscosity should matter in the model.

*We clarified this point (line 84).*

5) Line 94: Add references after “promising avenue.”

*Actually, the references were the topic of the remaining of the paragraph. However, we agree that it was misleading. Thus, we made it clearer (line 94).*

6) Lines 94-95: Seems like many of the concepts presented in this paper have been described elsewhere, so authors need to highlight the novelty of this study.

*We added a couple of sentences to clarify this point (lines 119-122).*

7) Lines 100-101: The use of the words “physical properties of the medium” would be informative to list in the title.

We changed the title accordingly. The title is now: “Inferring size-based functional response in aquatic and terrestrial systems from the physical properties of the medium”.

8) Line 105 (and elsewhere): Don’t forget the period and comma after “et al”.

*We corrected these typographic errors.*

9) Line 122: Clarify what is meant by “…attack rate and handling time would become emerging properties of the model.”

*We modified the corresponding paragraph to make it clearer (lines 126-130).*

10) Line 127: Should add “and the medium” (or some such statement) after “related to body size” (because it’s not JUST body size that is being considered).

*We followed the suggestion.*

11) Line 132: Can authors give a quantitative value for what they mean by “fits data remarkably well”?

12) Line 136: Unclear which model is meant by “this model”. The one in Portalier 2019 or the one in the current ms?  
*It is the Portalier et al. (2019) model. We clarified this point.*

Main framework & Validation of the model  
13) Line 140: The addition of “physical features” should be highlighted.

*We modified the paragraph as suggested (lines 150-154).*

14) Line 164: Can authors add a quantitative way to look at how well the model fits the data?

15) Line 184: Shouldn't the equations allow for type III FR also?

*Yes, equation 4 could allow for a type-III. In the Portalier et al. (2019), we use an encounter rate model that leads to a type-II. But if another encounter rate model is used, we could compute a type-III functional response. We clarify this point in the manuscript (lines 190-191).*

16) Line 188: For brevity, remove “in order”.

*We removed “in order”.*

17) Lines 189-190: Seems like personal notes that should be removed.

*The reviewer is right. We removed this point.*

18) Line 194: “It appears that the model fits the data quite well” is not at all convincing. Need a quantitative measure of model fit (e.g., goodness of fit, residuals, model skill).

19) Line 195: Seems like there are quite a lot of data for organisms in the mg size range and below, so this is not a valid reason. Seems like the model needs to change to include small organisms.

*We agree with the reviewer. We modified the paragraph accordingly (lines 208-210).*

20) Line 197: Handling time is very far off and the model for this needs to be changed.

*We changed the sentence. The end of the corresponding paragraph discusses the fact that handling time is not related to mechanical factors from the medium, and thus it should be investigated differently.*  
Conclusions and future directions  
21) Line 206: Not convinced that this model is useful for this type of prediction.

*Our point is to discuss possible hypothesis that would explain the discrepancies between predicted and observed handling time. We agree that the model does not provide a way to test them, but as we mentioned earlier in the text, any discrepancy between model and data can be explained as a missing element that should be included in the model.*

22) Line 221: Again, not convincing to just state that the model fits data well. Model may be of little value if authors cannot quantitatively demonstrate that the model processes fit real data well.  
  
Figures  
23) Line 392: The relationship of the real data looks like it could be modeled as a sigmoid function in Figure 1.

*Our model tries to be general across a wide range of sizes. However, it is possible that small organisms experience supplementary constraints that are not included in the model, which results in an overestimate of their speed. Similarly, larger animals may show specific adaptations (such as lubrification of the body) that increase their speed, and that are not size-related. These factors are not included in the model in order to keep its generality.*

24) Line 396: Can something be added to have the model asymptote at large sizes?

*Hirt et al. (2017) included a limitation for large animals due to limitations of quickly available energy. We did not include this mechanism in our model because we were more interested in general principles. However, it might an interesting aspect to consider in the future.*

25) Lines 399-400: This wording is repetitive of what's in the text and can be removed here.  
*We removed this sentence.*

Concluding Remarks:  
Authors need to focus on highlighting the novelty of the study and also providing quantitative evidence of model fit to convince the reader.

**# Reviewer 3**  
EVALUATION  
Please list your revision requests for the authors and provide your detailed comments, including highlighting limitations and strengths of the study and evaluating the validity of the results, and data interpretation. If you have additional comments based on Q2 and Q3 you can add them as well.  
General comment:  
In this manuscript the authors present a model that derives functional response parameters from allometric relationships of predators and prey and physical properties of the surrounding medium. The model is tested against published data from two recent meta-studies and a couple of additional original studies.   
I think this is an interesting study but I have a few major concerns and also a couple of minor comments about this manuscript that need to be addressed to improve its quality and comprehensibility. See my comments below. Overall I think this will be a valuable contribution to the field after a solid revision.   
General suggestions:   
One think that was not really clear to me and which I think is most important for the overall evaluation: how is this new study related to the previous study Portalier et al (2019)? Which parts of the model framework are maintained compared to this study and what part is truly novel here in the new paper? It seems that the consideration of the physical properties of the medium should be the novel part now but some considerations to this respect have been included in the previous study as well, as far as I understand.

*The original model is static. It computes time expenditure (for searching, capturing and handling) and energetic expenditure. The present model uses only part of the original one to compute time expenditure, but it accounts for variation in prey abundance. We clarified this point (lines 142-146).*

Moreover, I found that considerable parts of the relevant literature need to be considered (and cited) in the revised manuscript, see detailed examples below.

*We added several references, following the reviewer’s suggestions.*

A minor general point that I see missing from the discussion is the differentiation between foraging modes of predators. There are numerous studies that consider sit-and-wait predators versus actively foraging predators in the context of functional response studies (e.g. Twardochleb et al. 2020). In these either prey or predator velocity are main drivers of interactions. I think this has important implications for the model presented in your study and the underlying mechanisms need to be discussed here.

*We added a paragraph to address this point in the conclusion section (lines 261-267).The model assumes that both the predator and its prey move and can detect each other without any interference. This does not hold for sit-and-wait predators. The model can be adapted to compute an encounter rate in the case of a moving prey and a non-moving predator, but behavioral aspects such as hiding are not size-related, and therefore are not included in the model, although it could be a potential way to improve it.*

Specific suggestions:   
p.2 l.37: I would suggest to cite one of the earlier papers by Holling here, i.e. (Holling 1959)

*We added the reference.*

p.4 l.68: also see (Pawar et al. 2015)

*We added the citation.*

p.4 l.68: I suggest to write “or habitat complexity (Barrios ...)” or alternatively “or structural complexity (Barrios ...)”

*We added “habitat complexity”.*

p.4/5 ls.78-91: for the whole paragraph please also consider the publications by Beveridge and colleagues (Beveridge et al. 2010a, b) which seem very relevant in several aspects of this work.

*These two papers are relevant indeed. They are now cited in the corresponding paragraph.*

p.5 l.98: (Pawar et al. 2019) is not listed in the bibliography

*We added the full reference.*

p.5 l.99: maybe also consider the very recent publication by Cloyed and colleagues here (Cloyed et al. 2021)

p.7 l.138: by giving this explicit reference to pelagic organisms do you mean the model does perform worse for all other kinds of interaction types? This is also relevant in terms of the Pawar et al (2012) terminology where pelagic interactions as 3D/3D interactions are different than 2D/3D or 2D/3D interactions. Should be considered.

*The model assumes that both predator and prey move within the fluid, and cannot hide from one another. This is why the model is well-suited for pelagic or flying organisms. Interactions occurring on the bottom of the system (i.e., benthic or terrestrial systems) violate these assumptions (e.g., the predator can hide). We clarified this point in the corresponding paragraph.*

p.9 l.176: At least for ectotherms digestion is not independent from the physical property temperature (Rall et al. 2012). As you point out correctly, digestion is an integral part of the mechanisms subsumed in the handling time parameter. Please clarify.

*We agree with reviewer that this point needed clarification. We meant that it is independent of the mechanical factors included in the model (i.e., gravity, density, viscosity). We clarify this point in the corresponding paragraph (lines 181-184).*

p.9 ls.189/190: this seems like instructions from authors to authors themselves. This needs to be cleaned up!

*The reviewer is totally right. We removed this part.*

p.9 l.190: I see that the references are listed in the data files on GitHub but why not include them in the supplementary materials?

p.11 l.233: please also add (Jeschke 2007)

*We added the reference.*

**# Associate editor**

Dear Dr Portalier,   
  
The paper has now been reviewed by three reviewers. I agree with Reviewers 2 and 3 in that this manuscript has the potential to be a valuable and interesting contribution, but that substantial revision is required.  
  
Specifically, I agree with Reviewers 1 and 2 in that the manuscript requires quantification of the model fits. While the text and figures are helpful for describing and depicting the general trends, at this stage there is no quantification of how well the modeled parameters match the empirical data which significantly weakens the model validation section of the manuscript. Please ensure that you provide a complete list of references where you obtained the data for model validation in your Supplementary Material (Line 189-190).   
  
In addition, Reviewer 3 points out a substantial amount of relevant literature that should be considered (and cited) in the revised manuscript. This reviewer further points out that predator foraging strategy (sit-and-wait vs. active foraging) can substantially impact the functional response, which likely has substantial implications for the model presented in this manuscript. For example, depending on predator foraging mode it may be that prey or predator velocity is the main driver of the interaction. Please take some time to review the list of papers provided, and, where appropriate, incorporate some discussion of additional factors not considered in your model that may be relevant.

*We followed suggestion from reviewer 3. We added the relevant literature suggested, and we added a paragraph to discuss the case of sit-and-wait predators.*  
  
Each of the reviewers pointed out that the novelty of this work could be better articulated. Reviewer 3 has specifically asked that you address how this work relates to the previous study Portalier et al (2019), and how the material presented here is novel relative to the processes modeled in that paper.

*We clarified this point.*  
  
Below I have included a few additional comments / questions of my own:  
  
The effects of predator density on a predator’s per capita kill rate are now generally thought to be widespread. This mechanism is mentioned only in pasting towards the end of the manuscript (line 239-241). I agree that one could include other aspects associated to predation such as behavioral features into the model, but the reader is left wondering how this might be done or how it would improve model predictions. Which biological features specifically do you anticipate being important in reconciling the discrepancy between the predicted / observed data you present, and why? My suggestion is that you consider briefly describing how incorporating the biological part (e.g., interference) could help explain discrepancies in observed vs. predicted parameters, and /or be built into this modelling framework.

*As mentioned earlier in the manuscript, the main source of improvement would come from a better mechanism for handling time (especially prey subjugation, and predator satiation). The fact that smaller predators show a greater attack rate than predicted also suggest that improvement is needed in either small predator motion or prey detection.*  
  
Within the proposed framework the functional response behaves as a Type II response, yet we know that other forms of the functional response better match empirical data sets. Interestingly, there has been some recent work indicating that crustaceans exhibit nearly double the proportion of sigmoidal functional responses (Holling type III) as compared to predatory fishes (Dunn and Hovel 2020 Biol Lett). To what extent could the discrepancy in observed vs. predicted handling times be related to taxonomic differences (e.g., invertebrate / vertebrate)? Moreover, Vucic-Pestic et al (2009) found that variation in predator–prey body-mass ratios could also impact the shape of the functional response (Type II vs. Type III). I think there would be value in briefly discussing if / how your framework might be revised to consider distinct functional response shapes (e.g., by altering assumptions within the underlying model).

*We agree that other types of functional responses should be considered (as reviewer 2 also mentioned). Actually, the model uses an encounter rate model from the literature (Rothschild and Osborn, 1988). This model leads to a type-II functional response. Another model that would change encounter rate would need to another type of functional response. We addressed this comment in the revised manuscript.*