

The main goal of the article is to introduce a new model: a generalized functional response model that incorporates nonlinear modifiers (such as prey size) for when there are multiple predators. A second aim of the article is to show that regarding multiple predator effects (MPEs) the variation in prey-size and its effect on feeding rates are not often accounted for, and that crucially the expected prey survival can be biased if this effect is not considered.

The article is generally of interest and shows promise. However, it is also lacking in some aspects (summarized in this paragraph but see also the more detailed review below). In the current write-up some information needed for a complete understanding is missing which makes the article less accessible to a broad audience. The sometimes unclear presentation also applies to the carried-out simulations and might have caused me to misunderstand part of the model. Also, the introduction of the model, the literature review and the simulations done to show the biasedness of the MRM all feel a bit disconnected to each other. Further, and more importantly, the authors do not test their model on actual data, but only used it to generate data with which they show that the MRM can be biased if there is a certain structure to the data. I am not convinced that this is enough to show the usefulness and practicality of their model.

The model

The proposed model is based on binning prey abundances based on nonlinear modifier s into the vector of abundances \mathbf{C} (as stated in line 88) and then estimating the predator feeding rates in this classes by giving the predators preference on prey based on the value of the nonlinear modifier s . In the presented version of the model, this is done by modelling the attack rate as a function of parameters d and γ that co-determine the attack rate $a(\alpha, d, \gamma, s)$. I have the following questions and remarks regarding the model:

- Given that s is likely to be a continuous variable (such as prey size), how is the discretization of prey abundances into levels of s done and how does this impact the model fits? When the discretization is done is s the mean within a level, or the median, or something else?
- Based on the notation used, it appears that the prey consumption in a given level of s is modelled to be independent of the abundances of prey in the other levels of s . If this is correct, please justify this assumption. If this is not correct, please improve the notation used (e.g. bold characters for vectors and matrices).
 - If, following the previous point, the prey consumption within a given level of s is independent of the prey abundances at other levels, as I understand it this means that the functional response model is fitted separately to each prey class (if this is not the case, you could ignore this point – or clarify it). And if this is the case, I am not convinced that modelling the attack rate as the function of three parameters and the nonlinear modifier s is better than a more parsimonious model, such as (the simplest model) $a(\alpha, d, \gamma, s) = \alpha$ within a given level of s . The author should explain why their model is better/needed.
- if I'm not mistaken the simulation done in this studies do not include the last term appearing in equation 1. I am not convinced by the usefulness for the readers of adding terms to an equation that are then ignored. I suggest having a section "Extending the model" in the supplementary material for these terms and as well for

the other extension or modifications the authors mention dispersedly throughout the text. Equation 1 can then be presented the way it is actually used, which improves the clarity of the text.

- L136-137: please explain what the diffusion term does to make the text more accessible to a more general audience. In other words, why is it needed, how is it estimated, etc.
- The symbols used in equation 1 and the symbols used in the text do not match. Please use a consistent mathematical notation.
- What are the units of $g(s) \frac{\partial c}{\partial s}$? $\frac{\partial c}{\partial s}$ has the units “abundance per unit of s ”, but following equation 5, g is not dependent on s , so it does not compute. Please clarify.

The simulations

The description of the simulations should be more transparent:

- The model (equation 1) is based on discretising prey into classes based on a nonlinear modifier, in this case being the prey size. In the paragraphs about the simulations (starting at L187) nothing is written about how this was simulated. How many prey size classes were there? How were the survival rates summarized across prey size classes? Or have I misunderstood, and the prey size classes were not actually modelled and just the parameters of the attack rate were varied? But then how can you assess the bias of the models if it is limited to one prey size? Does it not depend also on prey size? This needs clarifications.
- Based on the example code provided, it seems that the simulations were done with a prey starting abundance of 100. But as prey per capita consumption is a nonlinear function of prey abundance (and in this case of prey size), the starting population size does affect survival rates. I have not seen this mentioned in the article. It is similarly to the length of the trials (the simulations), which in Figure 2 is varied. Please do the same for the starting population and justify starting values in the main text.
- The simulations are done without any source of variation/error, providing essentially perfect data which is very unrealistic. I would be interested in whether the found biases would also be found in a more realistic setting where there is a source of variation (such as biological variation or measurement error).

Use of the model and comparison with MRM

- In the study, the proposed model is used to simulate data, which is then used to assess the biasedness of the MRM. It seems that it is already known that the MRM does not give precise prey survival estimates (because of the reasons explained by the authors). Despite this, the MRM is still being used so it is good that the authors show that the MRM is biased if a prey-size effect on the functional response is present. But the authors should also show more evidence that this method (MRM) is still being used by researchers by citing more recent cases of its use (the citations at lines 49-54 are all rather old, with the exception of the self-citation). Given that the authors already do a literature review about MPEs and prey size, they could also report how many of the found studies used the MRM.

- By only creating simulations based on their model, the authors do not directly test their model: they do not show that their model improves the functional response estimation with real data or at least with simulated data not based on the model itself (i.e., independent data). The authors need to test their model to show that it is not just useful as a way of simulating predator-prey data with a prey-size dependency. This is currently not done. This is not the same as showing that the MRM is biased under certain conditions. I am also wondering whether there are not other more sophisticated model than the basic MRM (but not quite as complex as the presented model) to which one could compare this new model. This would make for a much more interesting comparison.
- Connected to the previous point, the title “Incorporating nonlinearity with generalized functional responses improves predictions of multiple predator effects” seems a bit out of place as no prediction with the new model is done. Prediction in the article is done with MRM, not with the new model, so in my opinion this is not enough for the reverse conclusion that is presented in the title.
- I think a useful section (maybe in the supplementary) would be one about how an experimental design must look like so that the presented model can be fitted. Of course, this cannot be done in great detail, but considering the complexity of the model (i.e., the considerable number of parameters) and also that there are multiple levels of s , already an indication of how many data points are necessary per level to fit the model would be useful for researchers that are planning on using this model.

Other points (in approximate order of appearance):

- L16: “myriad pathways”: some examples would be interesting.
- L19: space missing before citation parenthesis (here and in multiple other instances)
- L24: citation missing
- L69-73: citations missing.
- L81: the authors should put more emphasis on the fact that they make the assumption of no predator interference and should also justify it. I suppose the justification is that the focus of the article lies on showing the effect of nonlinear modifiers on the feeding rates. However, inter- and intraspecific predator interference is arguably as important as nonlinear modifiers, or more important.
- L83-84: “size-dependent [...] prey somatic growth (g)”. I think it is supposed to be “nonlinear modifier (s)-dependent prey somatic growth (g)”, as it appears as “ $g(s)$ ” in equation 1.
- L97: in this equation E appears to be independent from P_i , but in equation 1 it is written as $E(C, s, P_i)$. I suppose that the righthand side of the equation needs to be multiplied with P_i , as otherwise the per capita consumption is not scaled to the population level. If you model $P_i = 1$, add P_i anyway and specify that in this study it is $P_i = 1$.
- L135: specify that T = time.
- L147: The literature review feels a bit disconnected from the rest of the article. The authors should introduce it better, i.e., explain why it was needed/done.
- L159: the authors should report in how many of the reviewed articles the MRM was used, as one of their main messages is that the MRM is biased.

- L170: clarify “survival”: Please specify whether this is the survival **rate** calculated as the proportion of prey abundance at the end divided by the prey abundance at the end or whether it is something else.
- L194: you do not define the “degree of mismatch”. I guess it is one minus the other (basically the rate difference), but other measures are possible (e.g. the relative rate: survival in one group divided by the survival in the other). Please clarify and justify in the text.
- L201-202: for text clarity, I suggest moving this sentence to an earlier place to better explain to the readers what is done and why it is done.
- L210: the authors mention “three ways”, but in the following lines there is only a “First” and a “Second” which can be confusing. I realize that the “Second” is about two ways, but I think the clarity of this section can be improved.
- L231: please add the references of the 119 studies to the Supplement 1.
- L278: citations missing
- L283: here and elsewhere: how did the authors determine that a difference in 10% is a significant difference in estimated survival? Is there any way of quantifying whether this a significant difference (this is tied to my remark elsewhere of there being no source of variability in the simulations)? How much does a difference in 10% matter? The authors should address this questions either by modelling them or by discussing them.
- Figure 1:
 - The sentence “Panel C demonstrates how changing which determines ...” does not make sense.
 - A vertical line at $d=8$ in panel C could be a nice way of showing that this is where the attack rate is maximized.
 - Why is $d=8$ used in panel C when it is not used in panels A and B?
- Figure 2-4: in addition to being heat maps, these figures are also contour graphs.
- Figure 3: the caption says that “Each facet displays [...] for three different focal prey sizes”. I do not see three different prey sizes in each facet. Do the authors mean that each facet displays a different prey size? But as far as I understood d is a parameter that “scales the maximum attack rate according to the most vulnerable prey size” and the prey size itself. Please clarify.
- Fig S1: I suggest binning by year (it seems to be weirdly binned by approx. 0.7 years)