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PCIEcology

Dear Dr. Barraquand,

Thank you for the additional suggestions you have made to help us improve our manuscript. Please find our response to each suggestion below. In brief, we have incorporated them all.

Sincerely,

Mark Novak

P.S. Since we do not mention it in our responses below, please note that we increased the number of bootstraps from 50 to 100 since submitting the manuscript's prior version. As anticipated in our response to the first review, the consequences of doing so were inconsequential; the estimated effect sizes were changed only every so slightly.

> *Thank you for this revision of your preprint, and apologies for the delay.*
>
> *The added analyses and derivations make for a more comprehensive manuscript. The manuscript writing has been improved in many places, though I still have a couple of suggestions which I would like you to consider below (including revising some of the v2 edits where these may be improved). Please address each issue raised in your response letter.*

[Pt.1] *Please also number all displayed equations. I have seen your answer to referee 2 on using selective numbering for emphasis, but all equations that are not embedded in text need to be numbered. The equations which you find important now may not be the only ones that your readers may need to refer to in the future.*

Response: Change made as suggested.

[Pt.2] *l. 5 Please keep "Type I" in "Holling's original rectilinear Type I model". Otherwise your readers may wonder what rectilinear means in that context, or if it is a type II variant etc.*

Response: Change made as suggested.

[Pt.3] *l. 10 "Holling's linear and rectilinear models" Actually the only type I that should be attributed to Holling is the rectilinear, since Holling himself did not suggest to use the Lotka-Volterra type I. Please be mindful of this throughout the manuscript. Two options to fix the sentence are to replace "Holling's linear and rectilinear models" by "linear and rectilinear functional response models" or to solely state that "The multi-prey model clarifies the empirical relevance of Holling's rectilinear model" (I am not convinced that the multiprey model clarifies the empirical relevance of the Lotka-Volterra type I functional response, though it quite clearly shows the relevance of Holling's type I).*

Response: We broadly agree and have revised text throughout the manuscript accordingly. The issue of attribution and terminology is nonetheless made tricky by the fact that Holling didn't specify an equation for the rectilinear form and also used the term Type I in reference to the linear Type I model, often contrasting his disc equation with the work of Lotka and Volterra. In Holling (1965; pg. 12) for example, he stated that the Type I can be obtained by setting the handling time parameter of the Type II to zero.

[Pt.4] *l. 12 "support for the presence of linearity" -> "support for linearity"?*

Response: Change made as suggested.

[Pt.5] *l. 13-14 "find evidence that larger predator-prey body-mass ratios permit predators to search while handling greater numbers of prey". I am afraid that this statement is a stretch: the manuscript provides evidence that n is (weakly) correlated to higher predator-prey body-mass ratios, which could happen for a number of reasons, including handling greater numbers of prey when one is a large predator eating small prey, but not restricted to it. True evidence for handling a larger number of prey items when these are small would require actual observations of the "handling" process in addition to the fitting of the phenomenological, aggregated functional response. Please rephrase accordingly. A possibility would be to replace "find evidence for" by "find support for the hypothesis that..."*

Response: Change made as suggested.

[Pt.6] *l. 21 "but also that that more bounded conclusions should be drawn in theory presuming the Type I to be appropriate". The repeat of "that" should be removed. Additionally, I am not sure what the sentence means, especially what is a "bounded conclusion". I would suggest to rephrase.*

Response: Typo removed and sentence rephrased.

[Pt.7] *l. 23 The "Type 0 functional response" keyword should be justified l. 39-40 but the reference by Denny (2014) that comes afterwards does not mention the type 0. Unless you provide a mainstream reference (or preferably several) that clearly refers to the rectilinear type I as being a type 0, please remove "type 0" from the keywords.*

Response: We have removed the term Type 0 entirely, having now found papers using the term to refer to not just the rectilinear Type I, but also the linear Type I and an intercept-only "prey-independent" model!

[Pt.8] *l. 43 The reference to Holling 1959 points to Holling, C. S. (1959). Some characteristics of simple types of predation and parasitism. The Canadian Entomologist, 91(7), 385-398.*

That is the reference that defines the disc equation of the type II. Here I believe that you want to refer to the article defining the three types of functional responses instead:

Holling, C. S. (1959). The components of predation as revealed by a study of small-mammal predation of the European Pine Sawfly. The Canadian Entomologist, 91(5), 293-320.

That corresponds to Holling, C. S. 1959a in Denny 2014.

Response: Change made as suggested. (Thank you for catching this error!)

[Pt.9] *l. 87-88 "Holling's traditional functional response forms." Holling's rectilinear type I could be viewed as 'traditional' by some readers. Here I believe that it would be better to revert to the previous wording that mentioned "linear type I and type II" at the same position in that sentence. Again we can refer to the type II by Holling's name but the only type I that can be referred to by Holling's name is the rectilinear one, even though many authors have mistakenly associated the Lotka-Volterra-style type I to Holling's name. Lotka-Volterra type I is a possible synonym for strictly linear type I.*

Response: Change made as suggested (as well as in other places in the abstract and text), but we now also explicitly include the Type III (to which we were attempting to refer as well after including it per Reviewer 1's suggestion).

[Pt.10] *l. 240 "could be included because for them n and φ could equal 1". Unsure what is meant here – if $n = \varphi = 1$, then we get the type II.*

Response: The sentence was unnecessary and has been removed to avoid confusion.

[Pt.11] *Figure 6 legend. I would refer to an "Ito stochastic differential equation" rather than a "Ito integral process" to avoid confusion.*

Response: Change made as suggested.

[Pt.12] *l. 380 "a significant region of linearity". I would suggest "a region of linearity".*

Response: Change made as suggested.

[Pt.13] *l. 382 "confirm Sjöberg's hypothesis". This sounds a bit too strong, given that we do not have additional observations of predator-prey pairs with higher ppbm handling more prey items in the field, just the phenomenological functional response model fits. Also given the noise acknowledged l. 409. Try "support Sjöberg's hypothesis"?*

Response: Change made as suggested.

[Pt.14] *l. 440 "saturating curvature at low prey abundance". I am not sure that the wording is very clear. Do you mean concave and increasing with prey density at low prey abundance?*

Response: Change made as suggested.

[Pt.15] *l. 452-458 It is not clear to me whether this paragraph refers to the Lotka-Volterra type I or the rectilinear one, i.e. Holling's original type I. Perhaps this paragraph could be deleted as it does not bring a clear argument (in my opinion). The next paragraph is not much clearer and I would recommend to end that subsection l. 451, which promotes more testable statements.*

Response: Paragraphs removed as suggested.

[Pt.16] *l. 532-535 The present manuscript nicely demonstrates how questioning basic assumptions (such as here the exclusivity of handling and searching) can change ecologists' mindsets about the relative relevance of their standard models, which is hinted at in the first part of the sentence. The second part of the sentence suggests that improved communication between theoreticians and empiricists will benefit Ecology. I am not saying that it isn't true of course, but it comes a bit out of the blue as the grand conclusion of this paper. Especially given that all authors have – unless I am mistaken – already a foot in theoretical ecology and another in more empirical ecology. So I would suggest to stick to the first part of the sentence or rephrase a bit the conclusion.*

Response: The sentences have been removed and the formerly last two paragraphs have been merged to achieve a better ending to the paper.

[Pt.17] *Additional suggestions regarding the title*

Although I am in general reluctant to suggest title changes, I would ask to fix the revised (v2) title, which does not seem adequate for reasons explained below.

Reviewer 2 previously explained that the v1 title and abstract might unfortunately suggest support for the linear type I functional response of theoreticians while the paper provides mechanistic and empirical support for the rectilinear type I instead (and similar-looking smooth forms for finite n). I tended to agree, and expected to see a revised title mildly corrected to e.g. "In defense of the original Type I functional response: The frequency and population-dynamic effects of feeding on multiple prey at a time" (thinking of the original 1959 Holling paper with the definitions) or "In defense of the rectilinear Type I functional response: ...". The "In defense" in the first part of the previous title had the desirable feature that "feeding on multiple prey at a time" in the second part then appeared to be a mechanism to obtain the type I. Also, that is a catchy title with a nice historical twist to it.

However, I do not think that the new title, "Feeding on multiple prey at a time: The frequency and population-dynamic effects of functional-response linearity" helps reducing the ambiguity that reviewer 2 was worried about. The expression "functional response linearity" could still refer to the unbounded, Lotka-Volterra-style type I. Additionally, with this new framing, the reader might not guess at all how feeding on multiple prey items leads to such linearity. Meaning that many readers may not understand the title without reading also the abstract, which sounds undesirable. An easy solution may be to revert to the previous title with a minor correction as suggested above, making sure that one refers to Holling's version of the type I.

I have been pondering how one could alternatively clarify with minimal changes to your v2 title, if that is the preferred version. I could recommend starting with "Feeding on multiple prey individuals at a time" rather than "Feeding on multiple prey" since prey is not countable as a noun and there's a risk that the reader will immediately think "multiple prey species" [By contrast, mentioning the type I in the first part of the sentence, as with the v1 title, hints clearly that we are in a single-prey-species context]

Second, one could append "at low prey density" after "linearity". Then the reader will hopefully guess that feeding on multiple prey individuals of the same species at the same time, which is pretty unusual in the literature, might induce a special linearity at low prey density. That is a longer title though.

In my opinion, a minor correction to your v1 title may help the preprint/paper to reach its full citation potential. That said, provided that the title does not suggest support for a Lotka-Volterra type I (which would require different analyses as discussed previously), you can certainly pick a v2 variant or something else entirely.

Response: As suggested, the title now reads "*In defense of the original Type I functional response: The frequency and population-dynamic effects of feeding on multiple prey at a time.*" We have chosen not to include "rectilinear" in the title because Holling does not appear to have used that term in his writings.

Holling, C. S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada*, 45, 3–60.