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PCIEcology

Dear Dr. Barraquand,

Thank you very much for evaluating our manuscript and for finding such expert reviewers. We are grateful for the reviewers' suggestions and are pleased to hear that you are willing to consider recommending the manuscript. To summarize the primary changes we have made in response to the reviews, we have:

- included the Holling-Real Type III model (as well as a new generalization of the multi-prey and traditional Holling models) in the suite of models we evaluate;
- clarified our phrasing regarding the linearity of functional responses at low prey densities; and
- included more complete, step-by-step derivations of both the Type II and multi-prey model in the supplementary materials.

Detailed explanations of how we addressed these and all other suggestions follow below.

On behalf of my co-authors, I thank you again for your time and consideration, and hope that you find our revisions satisfactory. We look forward to your response.

Sincerely,

Mark Novak

Each comment and suggestion has been numbered and italicized, and is followed by our response.

Recommender (Frédéric Barraquand)

> *We have received two reviews of your preprint. The reviewers and myself find that your manuscript presents a convincing argument in favour of the multiprey model, which provides a mechanistic justification for functional responses that are linear at low prey densities, of which the rectilinear type I is a limiting case.*
>
> *However, the reviewers also highlighted a number of issues that should be addressed before I can write a recommendation. Please revise your manuscript accordingly, and provide a point-by-point response to all comments.*
>
> *Two points have especially caught my attention:*
>
> **[Pt.1]** *Mathematical simplicity aside, it is difficult to see any argument for the strictly linear type I functional response of Lotka-Volterra models, where quantities eaten can increase without bounds. Unless you show additionally that ahN stays <1 throughout numerous empirical time series (or for maximum N), I agree with reviewer 1 that arguments are provided here for the rectilinear type I response rather than a strictly linear one. I also concur with reviewer 1 that one should avoid calling the rectilinear type I "effectively linear", as one could argue the opposite when N spans the whole range of possible values, i.e., that the sharp angle of that function makes for a strong nonlinearity. Please make sure to edit the text accordingly.*

Response: We have made edits throughout the manuscript to clarify that we indeed intend for our phrasing to apply at sufficiently low prey densities. As the Recommender likely anticipated, we consider the inclusion of time series on the fraction of feeding individuals (ahN) to be beyond what our manuscript can accommodate. (Relevant data are forthcoming for a separate manuscript.)

> **[Pt.2]** *It could be worthwhile to also fit a type III response to empirical data as*

> *suggested by reviewer 2. In addition to the reasons mentioned by reviewer 2, it provides a comparison of the multiprey model to a similarly complex model, which allows to check that the model selection procedure is not just favouring more complex models (see also below). Although the type III could make parameter identifiability more difficult to obtain for some datasets, when prey abundances do not span the whole range of the functional response, I suspect that the comparison will help us get a more comprehensive picture of the support for the multiprey model.*

Response: We now include the Holling-Real Type III in our model comparisons. In fact, we now also include a new four-parameter generalization that simplifies to any of the traditional Holling models. Please note that issues with parameter identifiability motivated us to augment the two originally-used likelihood functions with a penalty term proportional to the values of φ (the Hill exponent) and n (see line 206 and the new section of the *Supplementary Materials*.) Please also note that we significantly reduced the number of bootstraps per dataset (see line 210). Doing so kept the runtime of our analyses including the two additional models to a mere two weeks and did not alter are prior inferences in any substantive way because the parameter point estimates remained well-estimated. (The analyses of our manuscript did not make use of previously-calculated parameter confidence intervals for which the much higher replication was needed for certain datasets.)

> **[Pt.3]** *l. 115-119 The derivation would be clearer with explicit derivatives written out and then set to zero, perhaps in an Appendix? See e.g. Leeuwen et al. 2007 Ecology 88(6), 1571-1581, Appendix A.*

Response: We now provide more explicit derivations of both the Type II and multi-prey models in the *Supplementary Materials*, referencing these on line 105 and line 118 of the main text.

> **[Pt.4]** *l. 197-201 While I support the use of BIC for finding the true model, I would also caution that consistency is an asymptotic statistical property. One way to safeguard against small sample sizes, potentially leading to too complex models being selected, is to check BIC selection against simulated data with commensurate sample sizes to the empirical data considered. Another option is to include in the model set functional responses of equivalent complexity to the multiprey model, like the type III. Yet another idea is to use the simpler rectilinear type I (piecewise) in the comparison against the type II, as suggested by reviewer 1, although the discontinuity might be a bit impractical.*

Response: We now include the Type III in our model comparisons to safeguard against this potential issue. The inclusion of our new four-parameter generalization further serves this purpose. The discontinuity of the piecewise rectilinear model did indeed prove to be too impractical to implement, which we suspect is an additional reason for why no one else appears to have used this model in the past.

Reviewer #1 (Wojciech Uszko)

> *It was my great pleasure to read and review the manuscript by Novak, Coblentz and DeLong.*
>
> *The subject of functional responses, although long present in ecological research, is full of intricacies that are often dismissed based on common beliefs, clichés or practices. One of them is the type I response that is typically considered empirically unrealistic but theoretically handy. The current manuscript addresses this issue by: (1) constructing a new functional response model (multi-prey model) of a predator that can handle more than one prey while simultaneously searching for other prey, (2) check for potential empirical relevance of the multi-prey model, and (3) show population dynamic consequences of the multi-prey model in the Rosenzweig-MacArthur model framework.*
>
> *I would like to praise the authors for a clear, solid and very interesting work they have done. Honestly, this article is one of the best ones I have read recently. As such, this work could be recommended and/or published as it is. My few comments and suggestions (see below) could make this manuscript potentially more appealing to a yet broader audience. At the least, I hope to learn something new, and look forward to hearing the authors' opinion on these matters.*

Response: We thank the referee for providing this positive summary of our manuscript!

> **[Pt.1]** *1. The authors fitted three models to the empirical data: type I, type II and multi-prey. I am wondering if there is a chance that for some data sets, a generalized Holling type III model (with the attack rate coefficient, handling time and exponent fitted) would perform better than the three other models. Intuitively, type III functional response curve can somewhat resemble the multi-prey response as with increasing exponent, a type III response looks like it saturates "faster" than type II, which multi-prey curves also do with increasing number of handled prey (with attack rate and handling time kept constant). Could it be checked if for data sets where the multi-prey model was found best fitting, a type III response performs better? I would be surprised if it does not happen in any of the data sets. This would of course slightly weaken the results of this study, yet it is something that the authors would not want to miss. Or why not fitting and comparing all four models (type I, II, III, multi-prey) in all chosen data sets?*

Response: Including the Type III and our new four-parameter generalization in the comparison provides some support for the Type III (as anticipated by the Reviewer) and little support for our new four-parameter generalization, but in our view does not weaken the strength of our conclusions. (We thank the Reviewer for pushing us to take these additional steps despite our original desire to avoid the Type III. The manuscript is satisfyingly more encompassing as a result.)

> **[Pt.2]** *On a more reflective note - I find it curious that both type III and multi-prey models offer a potential solution to the paradox enrichment for top-heavy systems by offering a potentially stable equilibrium at low prey densities. Note that type III has also been suggested to be more common for high predator-prey body size ratios (Hassell et al. 1977, Kalinkat et al. 2013, Uszko et al. 2015).*

Response: We now include these points with reference to the three suggested citations on line 185, line 445, and line 491. Interestingly, our analysis of the Hill exponent does offer support for the Hassell et al.'s hypothesis that Type III responses are more pronounced for higher predator-prey body-mass ratios (line 246).

> **[Pt.3]** *2. When reading the text, I started wondering early on: what does it actually mean to handle and search for prey simultaneously? What kind of predators would do that? I think many readers would think the same. The authors offer some insights to this first at the end of the discussion, but I would suggest to maybe mention some clarification in the introduction. If it is about literal handling, I would find it most reasonable to assume that handling more prey should decrease the search rate for other prey. On the other hand, if it is about digesting, it feels like this has been so far covered well enough by type II and III models (i.e., very short handling times if a predator, for instance a filter-feeder, can digest relatively many prey at the same time). Therefore, a couple of sentences about the empirical mechanics of the new model could be useful earlier on.*

Response: We understand the Reviewer's motivation and have added or rewritten text on line 67, line 118, and line 507 to address this suggestion, noting that much more extensive and precise discussions thereof have already been offered by the references cited therein. That said, and as evidenced by this new text and our manuscript as a whole, we explicitly disagree with the Reviewer's suggestion that digestion is *"covered well enough by type II and III models"*. Rather, these models specifically assume a process that is fundamentally unlike digestion in that they assume searching and “handling" (i.e. digestion) to be mutually exclusive.

> **[Pt.4]** *3. Can the authors draw any conclusions on where across taxonomic and functional groups the multi-prey model is expected to be a good candidate for a "true" functional response model? Is it possible to draw any conclusions about it from the analyzed data sets? Such information could be very useful for empiricists.*

Response: We had a similar thought while drafting the manuscript. This is what motivated us to perform the regression analyses presented in Fig. 2d in which we included the gross taxonomic identity of the four most common predator groups (representing 90% of all datasets) as a predictor variable. This analysis showed relatively minimal differentiation among groups from an effects-size perspective. Undoubtedly there is more to be explored (and similarly so for the now-added analyses of the Hill exponent), but unfortunately the FoRAGE database is not constructed with sufficiently refined and uniformly applied taxonomic categorizations to permit such an analysis at this point in time. An appropriate analysis would thus require considerably more effort with potentially little predictive insight.

> **[Pt.5]** *4. In general, I am wondering about what niche in ecological research the multi-prey could or should occupy. Would the authors suggest to add the multi-prey model to the "usual" set of functional response models that we fit to empirical data (i.e., type II and III, if there is saturation)? And for theoreticians - when should we assume the multi-prey response in our models? Should it be for specific systems? We know that small changes in functional response forms can drastically change model predictions (Fussmann and Blasius 2005), and I am wondering how a similar effect found here for the multi-prey vs. type I and II models could make our models more (or less?) robust and realistic.*

Response: We have no simple answer to this question and thus wish not to be prescriptive in the manuscript. Functional response models are used for many varied purposes and motivations ranging from simple data description to explanatory inference to predictions of various sorts, and there will never be a model that can or should serve all these purposes (even within each of the realms of empirical and theoretical work). Even more practically speaking, the analyses of our manuscript suggest little generic predictive power associated with the typically useful variables of predator taxonomy and predator-prey mass-ratio, so there is little guidance to offer — beyond that which we already offer (e.g., line 477) — on which specific systems any particular model is most appropriate for. (As our analyses also point out, the reality is not as simple as Type I responses being exclusive to filter feeders, as prior synthesis have concluded, for example.)

Regarding the sensitivity of model predictions, it depends on what one means by "*drastic*". As Reviewer 2 (**Pt.5**) alluded to, although the different Type II models studied by Fussmann & Blasius 2005 differ in their quantitative dynamics, they don't differ in their qualitative dynamics, with stochasticity blurring their distinctions even more. The multi-prey model (along with the other understudied models we discuss in the manuscript) differs from other models in the qualitative dynamics it can exhibit, making it useful for better understanding the general consequences of one's assumptions.

> **[Pt.6]** *5. (line 23) Should "type 0 functional response" be a keyword? Type 0 is never mentioned in the text.*

Response: We now include mention of this alternative name for the piecewise rectilinear model on line 38. (See also our response to **Pt.6** of Reviewer 2.)

> **[Pt.7]** *6. (lines 202-203) After the statement "Considering only those datasets that could differentiate among the performance of the three models", I suggest referring to the supplementary materials.*

Response: We believe the Reviewer is suggesting we refer to Fig. S2 of the supplementary materials, but have left the sentence unchanged because we believe Fig. 2(a-b) (referenced in the same sentence) to be more appropriate.

> **[Pt.8]** *7. (lines 202-210) The number "26%" that appears in the abstract should probably be mentioned also here.*

Response: We now do so on line 223 (noting that the number has changed somewhat due to the inclusion of the two additional models).

> **[Pt.9]** *8. (Fig. 2a) The labeling of the three circles is unclear. I guess it follows the color code as in panel b, but it would help if the labels were placed differently, e.g., "n-prey" and "Type I" on the sides, and "Type II" on top in the middle.*

Response: The updated figure avoids this potential source of confusion.

> ***Referee-provided references***

Fussmann, G.F. and Blasius, B., 2005. Community response to enrichment is highly sensitive to model structure. Biology letters, 1(1), pp.9-12.

Hassell, M.P., Lawton, J.H. and Beddington, J.R., 1977. Sigmoid functional responses by invertebrate predators and parasitoids. The Journal of Animal Ecology, pp.249-262.

Kalinkat, G., Schneider, F.D., Digel, C., Guill, C., Rall, B.C. and Brose, U., 2013. Body masses, functional responses and predator–prey stability. Ecology letters, 16(9), pp.1126-1134.

Uszko, W., Diehl, S., Pitsch, N., Lengfellner, K. and Müller, T., 2015. When is

a type III functional response stabilizing? Theory and practice of predicting plankton dynamics under enrichment. Ecology, 96(12), pp.3243-3256.

Reviewer #2 (Matthieu Barbier)

> *Thank you for the opportunity to review this manuscript. I am sympathetic to the mix of simple conceptual proposal, data analysis, and speculation on theoretical consequences, and I feel this article deserves to be recommended with only rather minor improvements - the main one being a clarification that the Type I functional response being "defended" here is not quite what most people have in mind.*
>
> *MAIN COMMENTS*
>
> **[Pt.1]** *1) This is my most important comment. One thing that makes the general framing a bit confusing is there being two notions of Type I here: the linear, and the rectilinear/piecewise which I had never heard of but seems to be the historical origin. This means that two distinct aspects of Type I could be defended and validated – being non-saturating over the whole range of observed abundances, vs being linear at low enough prey abundances within that range. You are quite crucially defending the latter rather than the former.*
>
> *The consequence is that you are not really reconciling Type II loving empiricists with Type I loving theoreticians and I would advise against insisting too much on that framing: provided we're in the abundance range where saturation is observable and this discussion matters at all, the kind of Type I that naturally arises as a limit of your model is the piecewise one, that neither side really uses and is probably not any better for theory than Type II.*
>
> *I also really hesitate to call that piecewise Type I "effectively linear" as you do a few times, as its nonlinearity is very stark and crucial for all the theoretical implications you mention. Incidentally, I am not sure that your "warning" to theoreticians improves dramatically upon what they already learned from Type II (except showing that having more complex nonlinearities allows even stranger behavior), so I would also downplay that a little bit.*
>
> *In summary, from the title and abstract on, I would advise you to be clearer in what you defend - not the absence of saturation of the commonly-used Type I (since there's not much new to say when we consider trajectories where saturation does not kick in at all), but a model that is closer to linear at low abundances yet still saturates.*

Response: We thank the Reviewer for this comment as it has helped us to clarify our intended message. We have made according changes to our phrasing throughout the manuscript (too many to list by line number). In particular, we have now more clearly distinguished between the linear and rectilinear models in our phrasing, clarified that our motivation was to understand how functional responses could exhibit linearity over a large range of (low) prey abundances (rather than just being well-approximated by linearity, as previous empirical work has suggested), and have replaced our use of the phrase "effectively linear" with more explicit wording. We have changed the title of our manuscript as well.

> **[Pt.2]** *page 9 "Incorporating this infinite power series into eqn. 1 shows that the expected proportion of predators handling prey at any given time will be ahN"*
>
> *I believe this is a calculation error, forgetting the 1/h. Clearly from (3), letting n-> infinity if ahN < 1 gives f(N) -> aN so either of the two statements must be false. If I am correct, then a few places discussing the consequences of this calculation should be adequately revised.*
>
> *(as a sanity check, I don't think that the same quantity could be either aN or ahN depending on the model, since those two expressions do not have the same units)*

Response: The Reviewer is correct that at the limit of $n \to \infty$, the *feeding rate* $f(N)$ given by eqn. 3 is aN (as we stated on line 157). However, the *proportion of predators that are handling prey* is given by eqn. 1 for which the limit as $n \to \infty$ is ahN (as we stated on line 159). These indeed do not have the same units. (In fact, for our own "sanity check" we note that $1/ah$ has the same units as N (see line 167), thus ahN is unit-less as any proportion should be.)

> **[Pt.3]** *3) For the theoretical analysis, it feels like your comparison class should include the rectilinear Type I as well, since your new model is an interpolation between that and*

> *Type II.*

Response: The piecewise nature of the rectilinear model makes it impractical to include in our statistical analyses (see also Recommender's **Pt.4**) and we do not have the mathematical expertise to formally analyze its dynamical consequences. (We presume the challenge of the latter is a reason why Seo and colleagues instead used the arctangent and hyperbolic tangent models in their work.)

> *MORE "PHILOSOPHICAL" COMMENTS*

> **[Pt.4]** *4) The theoretical analysis and results are fun, but I would not overinterpret the specifics – the realm of nonlinear dynamics has an endless bestiary of possibilities, and having bistability between a stable equilibrium and a limit cycle is but one among many things one could imagine happening with small variations around the original equations, so I do not know how much relevance should be ascribed to these results a priori.*

Response: Please see our response to the next comment, as we consider the motivations behind both to be closely related.

> **[Pt.5]** *5) The following is maybe a blanket comment regarding a whole subliterature and therefore not very relevant for any given article, but more and more people are making the argument that the intrinsic stochasticity of functional response could make fine details of nonlinearities less relevant (it feels like fitting a linear or saturating curve through a very hazy cloud of points should not lead to entirely different ecological conclusions). I am not yet entirely sure where I stand on this point, but it seems like something worth addressing at least in discussion.*

Response: We are aware of this literature on stochasticity. Indeed, it is this work that motivated us to perform the simulations underlying Fig. 6. That said, in potential contrast to the Reviewer, we see the literature to date as dealing only with models of the same general form having qualitatively equivalent stability regimes (e.g., Barraquand (2023), cited in our manuscript along with other directly pertinent work).

Our mathematical analysis show that the multi-prey model can exhibit qualitatively different stability regimes than traditional model forms, and that it shares these with two other, rarely-studied models of a similar form (and possibly the SSS model as well). Such insights are, to our minds, the ultimate goal of such theoretical analyses (see **Pt.4**). Our simulations show further that these contrasting qualities can in fact be consequential in the stochastic setting (Fig. 6), which we contextualized in the Discussion of our manuscript.

Though it feels too early to tell, we anticipate that the literature will eventually conclude that, in the stochastic setting, model form is by-and-large more important than model identity per se. The nuance will likely depend on what magnitudes and forms of stochasticity are most empirically relevant.

> *MINOR COMMENTS AND WRITING:*

> **[Pt.6]** *"Holling's original rectilinear Type I is dismissed by satisfying neither desire," -> clarify how it is distinct from the linear Type I (and perhaps why there are two different responses both called Type I?), otherwise this part can be confusing*

Response: The distinction is given on line 38 where we now also include the piecewise rectilinear model's alternative name (see response to **Pt.6** of Reviewer 1).

> **[Pt.7]** *page 5 and on: equations that are inline and without numbers make referring back to them a bit inconvenient.*

Response: We are sympathetic to the Reviewer's suggestion but have decided to retain our practice of numbering only the key equations of the manuscript in order to better highlight them. We hope that the explicit derivations now provided in the *Supplementary Materials* (see response to Recommender's **Pt.3**) will serve as a better place for interested readers to dig into and reference the component equations.

> **[Pt.8]** *page 7: "both multi-prey formulations" I see only one?*

Response: We were referring to eqns. 2 and 3 which differ in that n must be an integer in eqn. 2 but is continuous in eqn. 3, but this explicitness was unnecessary so we've removed it (line 155).

> **[Pt.9]** *page 8: "Further, the linear Type I is obtained when n infinity" the much more important conditon here is that $x<1$, which means effectively that h is short enough*

Response: Noting the potential confusion in regards the limit of $n \to \infty$ (see our response to the Reviewer's **Pt.2**), we do not see why the condition that $x = ahN < 1$ means that h must be "short enough" (which we interpret to mean short in absolute terms and thereby inconsequential). Rather, h can be arbitrarily large provided a is sufficiently small for any given N. The example we gave in Fig. 1 was for $h = 4$ and $a = 0.1$ with which $ahN < 1$ for $N \lesssim 3$ (illustrated with the solid black line), all of which are reasonably large (and demonstrably consequential) values.

> **[Pt.10]** *page 10: "for which no sufficiently-simple Lambert W solution could be obtained." You havent't mentioned Lambert W anywhere so this is a bit incongruous*

Response: This was intended for readers with technical expertise in using Lambert W to obtain closed-form solutions, but is not needed and so has been removed (line 210).

> **[Pt.11]** *"we excluded datasets for which the linear Type I had alone performed best" Perhaps recall that the 50% cases where the classic Type II was the best performing one correspond to n1 and can thus be integrated seamlessly into the regression.*

Response: We have now done so on line 239.

> **[Pt.12]** *Equations (4a) and (4b) do not mention the attack rate which is among parameters in Figures.*

Response: Equations 4a and 4b refer to a generic functional response $f(N)$, with the attack rate and handling time parameters having been introduced earlier for the specific formulation of the multi-prey model in eqn. 3. We also mention that we inserted eqn. 3 into eqns. 4 for our analyses of the multi-prey model on line 288.

> **[Pt.13]** *"Multi-prey feeding may thus be seen as another potential mechanism with which to resolve the paradox". Not sure it resolves the paradox, as you later argue (not that it's even clear that the paradox was something to be resolved in the first place, perhaps we could all agree to lay that framing to rest and not much will be lost - but that's only a suggestion)*

Response: Agreed. We have removed reference to any "paradox" throughout and have rewritten the two key sentences (line 323 and line 343) to avoid using this specific phrasing. We now refer to the "paradox of enrichment" (in quotes) only when first introducing the Rosenzweig-MacArthur model (line 80) since it is a common name given to this model.

> **[Pt.14]** *Throughout: I'm not sure that "information-theoretic" is a useful qualifier here (in the various places it appears) – using a BIC is not uncommon as a 'normal stats practice', and you do not seem to be relying on information theory beyond that.*

Response: Good point. We've removed the qualifier except in one place (line 373) where it remains appropriate.