





Peer Community In Ecology

Revising behavioural assumptions leads to a new appreciation of an old functional response model

Frédéric Barraquand  based on peer reviews by **Matthieu Barbier**  and **Wojciech Uszko**

Mark Novak, Kyle Edward Coblentz, John P DeLong (2024) In defense of the original Type I functional response: The frequency and population-dynamic effects of feeding on multiple prey at a time. bioRxiv, ver. 4, peer-reviewed and recommended by Peer Community in Ecology. <https://doi.org/10.1101/2024.05.14.594210>

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The functional response, describing the relation between predator intake rate and prey density, is a pivotal concept to understand foraging behaviour and its consequences for community dynamics. Holling (1959a) introduced three types of functional responses according to their shapes, labelled I, II and III. The type II, also known as the disc equation (Holling 1959b), has become popular among empiricists and theoreticians alike, due to its ability to describe predator intake saturation. The type III is often used to represent predator switching to other prey species when main prey density is low.

Although theoretical works identify the linear functional response used in Lotka-Volterra models as a type I, Holling (1959a)'s type I model actually envisioned that at some threshold prey density, the linear increase in predator intake with prey density would give way to an upper predator intake limit, so that Holling's type I has a rectilinear shape, with an angle joining straight lines. Ecology students can actually see this rectilinear shape reproduced in some textbooks, although not in textbook dynamical models, as they usually transition from Lotka-Volterra models to models with type II response.

To many, the rectilinear shape of the original type I looks like a historical curiosity: the type II functional response accounts for intake rate saturation with a more convenient smooth function.

Novak et al. (2025) turn this preconception on its head by first pedagogically showing that Holling's original type I model can be obtained as a limit case of a variant of the celebrated type II model. The derivation follows up earlier work by Sjöberg (1980), which might be unfamiliar to readers outside aquatic ecology. The often untold assumption of the type II functional response model is that searching and handling prey are two

exclusive behavioural processes, with predators that can only handle one prey item at a time. Allowing for several prey items to be handled at once while searching, until the predator reaches n prey items, the original type I functional response emerges as a limit case of the « multiprey » functional response as n goes to infinity. Interestingly, the multiprey response looks a lot like the original type I for large yet doable n .

Novak et al. (2025) then proceed to look for the prevalence of such multiprey functional response shapes in a large database of functional responses (Uiterwaal et al. 2022). Combining linear type I and multiprey models (the asymptote may not always be visible), they find support for this revised type I hypothesis in about one-third of the cases. Although the type II and III models are still well supported by data, the results do suggest that linearity at low prey density may well be more frequent than one thinks. They complement this analysis by showing that larger predators relative to their prey tend to have larger n in the multiprey response. It is consistent with the hypothesis that the bigger you are relative to your prey, the more prey items you can handle at once.

Finally, Novak et al. (2025) investigate the consequences of the multiprey model for community dynamics. They find overall a richer dynamical behaviour than the Lotka-Volterra type I and common parameterizations of the type II, suggesting that observed linearity in some range of prey density does not necessarily translate in simpler dynamical behaviour.

Novak et al. (2025) provide here a convincing and pedagogical study showing how seemingly benign behavioural assumptions can in fact profoundly alter the perceived relevance of community dynamics models. As they conclude, their analyses have lessons for future empirical functional response work, which should not necessarily dismiss the type I model and consider perhaps variants to the classical type II and III, as well as for future theoretical analyses, which could generalize this model to multiple prey species, or relax other behavioural assumptions.

References:

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

<https://doi.org/10.4039/Ent91293-5>

Holling, C. S. (1959b). Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, 91(7), 385-398. <https://doi.org/10.4039/Ent91385-7>

Novak, M., Coblenz, K. E., & DeLong, J. P. (2025). In defense of the original Type I functional response: The frequency and population-dynamic effects of feeding on multiple prey at a time. *bioRxiv*, ver.4 peer-reviewed and recommended by PCI Ecology <https://doi.org/10.1101/2024.05.14.594210>

Sjöberg, S. (1980). Zooplankton feeding and queueing theory. *Ecological Modelling*, 10(3-4), 215-225.

[https://doi.org/10.1016/0304-3800\(80\)90060-5](https://doi.org/10.1016/0304-3800(80)90060-5)

Uiterwaal, S. F., Lagerstrom, I. T., Lyon, S. R., & DeLong, J. P. (2022). FoRAGE database: A compilation of functional responses for consumers and parasitoids. *Ecology*, 103(7), e3706.

<https://doi.org/10.1002/ecy.3706>

Reviews

Evaluation round #3

DOI or URL of the preprint: <https://doi.org/10.1101/2024.05.14.594210>

Version of the preprint: 4

Authors' reply, 27 January 2025

Dear Dr. Barraquand,

Thank you for your careful reading of our manuscript (and for thereby spotting the remaining typos); they have all been corrected. I have also (1) updated the manuscript's title in the repository's README, (2) deposited the GitHub repository and Supplementary Online Material on FigShare, (3) included the repository's and SOM's FigShare DOIs on the manuscript's cover page and in the references. I've left the line numbers and information on the cover page as is (since journals will likely be requesting the same).

Thank you again for your time and effort. The manuscript has been greatly improved as a result.

Sincerely,

Mark Novak

Decision by [Frédéric Barraquand](#) , posted 22 January 2025, validated 22 January 2025

Dear authors,

Thank you for this revision of your preprint which appears to be almost ready to be recommended. The few minor points that remain are:

1/ I must ask for the code and data to be deposited to a permanent open repository before recommendation, following guidelines listed in section 2.3 here https://ecology.peercommunityin.org/PCIEcology/help/guide_for_authors Apologies for the delay, I spotted this rather late, after writing my recommendation. Please keep in mind to update "FigShare_url_posted_after_acceptance" accordingly in the Code and availability statement of your preprint (the github link is useful and can stay as such, it just needs to be complemented by a permanent DOI and URL). The Guide discusses how to connect GitHub to Zenodo, note that you can also connect Github to FigShare (or OSF) if more convenient or preferred. The preprint title in the README of the GitHub repository could be updated first.

2/ I spotted a couple of (small) typos to correct

l. 171 Of futher note -> Of further note

l. 173 extra outside parenthesis ")"

l. 519 Rosenzweig-MacArthur-> Rosenzweig-MacArthur

Supplementary. Between S4 and S5, "the rate at which each these P_H predators finishes handling its prey" -> "of" missing?

Please take this opportunity to fish for any other remaining typo.

3/ You may take this occasion to remove the linenumbers for a more polished look of your preprint on biorxiv (and to make other cosmetic adjustments if you wish, e.g. position in the manuscript of code and data availability/contributions/acknowledgements/COI disclosure, currently on 1st page), since there will be no more edits requested, and my recommendation will point towards this version.

Evaluation round #2

DOI or URL of the preprint: <https://doi.org/10.1101/2024.05.14.594210>

Version of the preprint: 3

Authors' reply, 20 December 2024

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Decision by **Frédéric Barraquand** , posted 16 December 2024, validated 17 December 2024

Dear authors,

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.

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.

I look forward to your revised version,

Best regards,

Frédéric Barraquand

Line-by-line comments

I. 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.

I. 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).

I. 12 "support for the presence of linearity" -> "support for linearity"?

I. 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 R_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..."

I. 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.

I. 23 The "Type 0 functional response" keyword should be justified I. 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.

I. 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.

I. 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.

I. 240 "could be included because for them n and ϕ could equal 1". Unsure what is meant here – if $n=\phi=1$, then we get the type II.

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

I. 380 "a significant region of linearity". I would suggest "a region of linearity".

I. 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 ppm handling more prey items in the field, just the phenomenological functional response model fits. Also given the noise acknowledged I. 409. Try "support Sjöberg's hypothesis"?

I. 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?

I. 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 I. 451, which promotes more testable statements.

I. 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.

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.

Evaluation round #1

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Version of the preprint: 1

Authors' reply, 15 October 2024

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Decision by [Frédéric Barraquand](#) , posted 02 August 2024, validated 03 August 2024

Revision

Dear authors,

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:

- 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.
- 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.

Looking forward to the revised version,

Best regards,

Frédéric Barraquand

— Some additional line-by-line comments —

I. 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.

I. 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.

Reviewed by [Wojciech Uszko](#), 03 July 2024

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. 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? 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). 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. 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. 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. 5. (line 23) Should "type 0 functional response" be a keyword? Type 0 is never mentioned in the text. 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. 7. (lines 202-210) The number "26%" that appears in the abstract should probably be mentioned also here. 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.

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.

Reviewed by Matthieu Barbier , 15 July 2024

Dear Authors,

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.

Sincerely,

Matthieu Barbier

MAIN COMMENTS

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.

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 $n \rightarrow \infty$ if $ahN < 1$ gives $f(N) \rightarrow aN$ 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)

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.

MORE "PHILOSOPHICAL" COMMENTS

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.

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.

MINOR COMMENTS AND WRITING:

"Holling's original rectilinear Type I is dismissed by satisfying neither desire," \rightarrow 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

page 5 and on: equations that are inline and without numbers make referring back to them a bit inconvenient.

page 7: "both multi-prey formulations" I see only one?

page 8: "Further, the linear Type I is obtained when $n = \infty$ " the much more important condition here is that $x < 1$, which means effectively that h is short enough

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

"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 $n=1$ and can thus be integrated seamlessly into the regression.

Equations (4a) and (4b) do not mention the attack rate which is among parameters in Figures.

"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)

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.