Peer Community In Ecology

A multidimensional exploration of predator-prey dynamics

Gloriana Chaverri (ID) *based on peer reviews by* **Thomas Guillemaud** (ID) *and 2 anonymous reviewers*

Submitted: 10 January 2024, Recommended: 16 December 2024

Cite this recommendation as:

Chaverri, G. (2024) A multidimensional exploration of predator-prey dynamics. *Peer Community in Ecology*, 100643. 10.24072/pci.ecology.100643

Published: 16 December 2024

In the preprint "From Fear to Food: Predation Risk Shapes Deer Behaviour, Their Resources, and Forest Vegetation", Martin et al. provide a comprehensive examination of the intricate interplay between predation risk, deer behavior, and forest ecosystems. The study offers notable insights into the "ecology of fear," as it takes advantage of an extensive dataset that reflects decades of dedicated research effort. The authors' approach combines behavioral ecology, plant community analysis, and stable isotope studies, making this work a significant contribution to our understanding of complex ecological phenomena.

One of the most striking aspects of this study is the scale and richness of the dataset. The authors used data collected over multiple decades, spanning various experimental contexts, including islands with and without predators, hunting, and culling histories. These datasets are invaluable, as such long-term, geographically diverse studies are rare. The inclusion of both behavioral observations (e.g., flight initiation distances) and ecological outcomes (e.g., vegetation recovery) underscores the effort to provide a holistic understanding of these ecological interactions.

The results are not only scientifically robust but also conceptually significant. They challenge simplistic assumptions about predator-prey relationships by illustrating how both the presence and absence of predation risk can have lasting effects on ecosystems. For example, the findings that culling restores vegetation but creates behavioral shifts in deer populations emphasize the complexity of ecological restoration efforts. These results invite further exploration into how behavioral adaptations to predation risk may alter long-term ecosystem trajectories.

In conclusion, Martin et al.'s preprint represents a significant advancement in understanding predator-prey interactions and their cascading effects on ecosystems. The study's comprehensive dataset and integrative approach provide a model for future research in ecological and behavioral sciences. It is a commendable contribution to the field, with implications for both theoretical ecology and practical conservation.

References:

Jean-Louis Martin, Simon Chamaillé-Jammes, Anne Salomon, Devana Veronica Gomez Pourroy, Mathilde Schlaeflin, Soizic Le Saout, Annick Lucas, Ilham Bentaleb, Simon Chollet, Jake Pattison, Soline Martin-Blangy , Anthony J. Gaston (2024) From fear to food: predation risk shapes deer behaviour, their resources and forest vegetation . HAL, ver.6 peer-reviewed and recommended by PCI Ecology https://hal.science/hal-04381108v5

Reviews

Evaluation round #3

DOI or URL of the preprint: https://hal.science/hal-04381108v5
Version of the preprint: 5

Authors' reply, 09 December 2024

Please find below our response to the third round :

All editorial suggestions have been implemented
Comment on risk presence and shoreline use
OK *see rewrite in lines 131-132*
Comment on absence of section numbers in Table caption
          OK *see lines 170 and 172-173 for rewrite*
Notes
We improved formatting of text in view of publication
We added a picture plus caption see lines 529-531

Decision by Gloriana Chaverri ⓘ, posted 03 December 2024, validated 03 December 2024

Dear Dr. Martin,
Thank you for carefully addressing the suggestions made by the two reviewers. Your current version of the manuscript is now in excellent shape.
I am suggesting a few remaining, mostly minor, changes that should be incorporated before I can accept it and write my recommendation. These suggestions have been detailed in an annotated PDF file.
I look forward to receiving your final version.
Best regards,

Download recommender's annotations

Evaluation round #2

Authors' reply, 22 November 2024

Please find attached a PDF file withe our reply

JL

Download author's reply

Decision by Gloriana Chaverri ⓘ, posted 17 October 2024, validated 17 October 2024

Dear Dr. Martin,

We have received the evaluation of two anonymous reviewers and they seem very happy with the changes you have made to your manuscript. I agree with them; the manuscript is much clearer now.

One of the reviewers still has some valuable suggestions that I hope you will find useful. I think, however, that the line numbers the reviewer is referring to do not coincide with those in version 4 uploaded to Hal. Please check the suggestions made and let me know if you have questions.

I also have some minor suggestions of my own (just to clarify some small issues or improve readability).

Line 115-116: I suggest you simplify this hypothesis a bit. Maybe something like "...would reduce fear in deer causing them to reduce forest vegetation cover and diversity."

Line 118: behaviour.

Line 203: sometimes.

Line 223: "to estimate".

Line 356-358: Please revise this sentence.

Line 402: parsimonious.

Line 403: "each sample".

Line 516: individuals captured.

Line 547: deer diet.

Figure 7: Some of the legends are not very clear (e.g., columns 1 and 2). Maybe you can use a single, and larger, legend, since colors are depicting the same categories for all graphs.

Figure 8: Can you also mention what the small dots represent?

Line 683: resources

Line 689: When you start the section on stable isotopes maybe you can separate this into a new paragraph.

Line 745: understories.

Kind regards,

Gloriana

Reviewed by anonymous reviewer 1, 28 September 2024

The authors worked well on the previous comments. I really like the paper and its contents. Yet the text (abstract, discussion) can be considered long.

Does the title clearly reflect the content of the article? Yes

Does the abstract present the main findings of the study? [ ] Yes, but the text is long.

IAre the research questions/hypotheses/predictions clearly presented? [ ] Yes, improved a lot.

Does the introduction build on relevant research in the field? [ ] Yes

Are the methods and analyses sufficiently detailed to allow replication by other researchers? [ ] Yes

Are the methods and statistical analyses appropriate and well described? [ ] Yes
Are the results described and interpreted correctly? [ ] Yes
Have the authors appropriately emphasized the strengths and limitations of their study/theory/methods/argument? [ ] Yes
Are the conclusions adequately supported by the results (without overstating the implications of the findings)? [ ] Yes, but more caution could be suited here and there.

Reviewed by anonymous reviewer 2, 05 October 2024

I thank the authors for their revisions. I believe the manuscript is much easier to follow in many places.

The manuscript feels a little lengthy. This is not a problem per se, but it makes it important for the authors to structure the writing in a way that help reinforce memory of the details (the sub-headers do help). Some of the thinking and writing still seemed a little disorganized.

The key section of emphasis to me remains the introduction, which I find a little ineffective. Lines 50-80 or so focus on some broad ecological problems, and ultimately lead to the following questions: (1) whether different metrics of behavioral risk response vary under the presence of hunting and natural predators, and (2) whether behavioral shifts influence how deer affect forest ecosystems.

What I broadly suggest is:

–I would condense much of Lines 50-80 into one brief paragraph. ("Hypotheses and evidence suggest that prey alter their behaviors in response to perceived risk, and also that shifts in prey behavior can have broader ecological impacts. Examples include…" [or "this is important because…", etc.])

–The next couple of paragraphs should set up the problem/uncertainty that motivates the research. Essentially, what is the story about? How deer behave on different islands in this region and what drives it? Some conceptual uncertainty or a question that extends upon previous work? Trying to summarize the results of many different sampling efforts? Reconciling information across disparate methods? I can't be very prescriptive here because this is the authors' work and I can't tell what they want to achieve, but this part is critical.

–Then, the authors conclude with the specific objectives and an extremely brief overview of how they resolve the motivating uncertainty ("we use X data from X islands to [test Y, describe Z, whatever]").

The authors are obviously free to craft the section as they choose. Regardless of how they proceed, it would be helpful to present a clearly defined problem that motivates the research and a quick description of how the problem is going to be solved. (In short, try to make sure readers can intuit what is going to be discussed later). The problem could be theoretical, or descriptive/system-specific, or applied, or methodological…any of these might work. As it stands, the introduction and discussion feel disconnected: the former briefly summarizes a few very broad topics, and then the latter introduces new concepts.

Line comments below.

L97: "contrasts in deer 97 behavior modify how deer affect the forest ecosystem…". Consider alternative phrasing. What is largely presented here is a comparison of vegetation characteristics across different islands, and there is an extra bit that has to be inferred (that these differences are attributable to deer) to make this connection.

L127: It would be great to add some additional columns to the table—where the flight distance info is available, where some of the other behavioral data was collected or not—rather than have this solely in the text. Don't have time as a reviewer to go through each subsequent section and try to figure out the specific contrasts that are testable for each analysis, and probably most casual readers will not either. Is there a "natural predators, no hunting" strata? If not, is it possible to distinguish between hunting and natural predation as sources of risk, or should these be acknowledged and discussed as confounding?

L166: Consider moving this to the end of the section…the later sub-headers all broadly focus on deer behavior, while the focus is vegetation here (and the presented questions are ordered as deer behavior -> ecosystem patterns).

L176: Is there an analysis that could be used to test the sub-header question given the seemingly very unequal variances (I can think of ways that would be easy to code from scratch, but not sure about standard r packages)? Otherwise, this seems a little fuzzier relative to the other sub-headers.

L193: I think "hypothesize" (or posit/speculate or similar) rather than "conclude". Wondered if Darimont et al.'s 2003 paper (https://doi.org/10.1139/z02-246) might be more appropriate to cite here than Darimont and Reimchen 2002. Also wanted to note again that these citations tend to focus on wolves undertaking marine-based foraging (salmon, otters, whatever).

I think what the authors are assuming (conceptually) is that wolves can quickly/effectively switch from one hunting state (i.e., looking for marine resources) to another (i.e, hunting ungulates). If so, the authors should lay out their thinking clearly. Note, there are other conceptual assumptions that could be made and these might be equally plausible: for example, a pulse of summer marine resources might make wolf space use more predictable (and thus easier for deer to avoid); broader availability of forage for deer during summer (at the same time that wolves are anchored to dens) might make such avoidance easier/less costly, and so forth.

L297: Might note some assumptions here associated with the sampling (i.e., via hunting, or looking < 1000m from shore).

L345: I think that with 2 markers and 4 sources, the results will be heavily dependent on the specified priors (multiple combinations of p_k, can produce the same observations given mu_jk and $sigmasq\_j$). It might be good to report these (or perform some sort of sensitivity analysis), or potentially even compress the sources into fewer groups. (I think that really only the marine and terrestrial groups are of interest?)

Fig 3.: It would be great if this was compared in a testable way (i.e., does composition statistically differ?).

L639: I think the submission should set up these sub-header questions more clearly in the introduction. Some of this text reads a little like post-hoc storytelling, and some of the topics like bold/shy deer (I suppose these are something like behavioral syndromes?) & the attenuation of behavior influencing densities seemed distinct from what the authors presented as the goals previously. I.e., if a main hypothesis of the paper relates to behavioral syndromes, this needs to be mentioned much earlier.

L746: These few sentences weren't entirely clear to me. Can the authors present their thinking further?

L753: While it wouldn't surprise me if natural predators also played a key role, it seems to me that the immediate evidence is that hunting is more strongly associated with reduced seaweed consumption?

Evaluation round #1

Authors' reply, 10 September 2024

Please find attached the pdf with our detailed reply to recommender.

Changes are identified with references to lines in response

As changes were extensive the usefulness of tracked changes became moot.

For the recommender and reviewer to be able to assess if we addressed their points we referred to the lines in the final revision were these points are addressed.

The current revision is the pdf document uploaded on HAL as last version.

Sincerely

Jean-Louis Martin

Download author's reply

Decision by Gloriana Chaverri ⓘ, **posted 29 March 2024, validated 03 April 2024**

Dear Dr. Martin,

We have finally received an assessment of your preprint "From fear to food: predation risk shapes deer behaviour, their resources and forest vegetation" from 2 anonymous reviewers. As you know, Thomas Guillemaud also provided a positive assessment of your data and script. I am sorry the revision took this long, but it was very difficult to find the two reviewers needed despite multiple invitations sent.

The reviewers and I agree in that the study is timely and highly relevant, and that the information provided is an amazing effort towards understanding how predation and hunting may affect the behavior of prey and in turn how changes in behavior affect plant communities. While we believe this study is worth publishing, there are several important issues that need to be addressed before I can provide a recommendation. Both reviewers suggest that structure and clarity need to be improved throughout. We also seem to agree in that some of the arguments in the discussion are not convincing or are highly speculative, and that the conceptual framework needs strengthening. I would like you to carefully consider our suggestions and, as one reviewer says, "dig deeper into the literature and think through things more carefully". This is a study worth publishing which still needs to be polished.

As you will see, both reviewers provide very useful suggestions that will certainly improve your manuscript. I also revised your manuscript carefully and am explaining my main concerns below. I also provide some comments and suggestions in the attached pdf.

My fist major concern is that the introduction lacks hypotheses and/or predictions that would allow the reader to critically assess your results on the basis of evidence from previous studies. I think you should at least have a hypothesis for each major section that contributes to the overall story you are trying to weave, that is, predators (or humans) increase fear in deer, which in turn reduces foraging in open areas, which then results in changes within plant communities. If I am indeed correct in my understanding of what the main topic of your paper is, then my impression is that you would need to have 2-3 hypotheses. The first hypothesis would be that predation and culling increase fear in deer (with all relevant studies that support this hypothesis). Then you can mention each prediction, based on what behaviors you are measuring: FID, Dtravel, use of baits, diel activity. You can complement this first section with findings on the proportion of marine algae in deer diet, but you need to be a bit more explicit about what to expect adding another hypothesis/prediction, ideally based on previous studies that show that deer (or other herbivorous mammals) in fact avoid open spaces, such as shorelines, in the presence of predators. With clear predictions of all these changes in behavior, especially avoidance of open spaces, then what would you expect to find in plant communities? Provide a clear hypothesis and prediction(s). For example, do we expect low understory cover overall, or do we expect to find changes in community composition because deer forage on specific plants? Since there were no predictions on this topic, it was difficult for me to understand the results.

Second, I think the result section can be significantly summarized so that you present the most relevant results to the question being posed. Many data could be presented as supplementary material without loss of information contributing to the paper's main question. There are also many redundant tables that could be removed. I also think that the way you present results of changes in vegetation (first section of results) is not very clear, which could in part be due to lack of predictions. I added a suggestion of a graph that could help, but please feel free to modify as you see fit. You are also presenting results of statistical analyses in a format that is not typical (adding raw results to the main text, not even within parenthesis), so I suggest you remove those data and include in a table (perhaps even as supplementary material), and maybe only keep p-values in the main text.

Third, a large part of the study relies on a set of results that, in my opinion, still need to be presented differently and/or explained in greater detail. I am referring to the results section "Understory vegetation varied with risk history". First, the way you quantify differences in plant communities is not clear in the methods section. Then results are also not clearly presented (see comment in previous paragraph). Finally, in the discussion you mention beta-diversity, which had not even been explained before. Since these results are

highly relevant to your study, I suggest you pay close attention to them. If I am correct in my assessment of these data, I think you are focusing on two separate issues: % understory cover (is the ground covered by a lot of smaller plants that could provide food to deer?) and species composition (how do composition of plant communities, like alpha and beta diversity, differ among sites). I do not claim to be an expert on the topic, but the results are nor overly convincing and I have seen many other ways to quantify differences in communities among sites that are not included in this study.

Fourth, in the discussion section you are speculating in various sections. This is primarily a problem in the section "Did (the absence of) risk affect the use of exposed habitats?", where you seem to connect deer behavior to the structure of plant communities, yet you did not explicitly test this. You extended this speculative argument to the abstract, saying that "the lack of costly anti-predator behaviors was not significantly affected by the presence of abundant and higher quality forage". Again, your data do not provide any support for this.

A final thought: I think you are presenting your results a bit backwards. For example, it seems that changes in behavior should go first, then how risk may modulate foraging in open areas (shorelines), and lastly how risk-aversion changes plant communities. I am following the order in which you presented your questions, which to me makes a lot more sense.

I hope our suggestions prove useful, and I am looking forward to seeing the next version of the manuscript.

Kind regards,

Gloriana **Download recommender's annotations**

Reviewed by anonymous reviewer 1, 26 March 2024

Does the title clearly reflect the content of the article? [ ] Yes

Does the abstract present the main findings of the study? [ ] No, clarity, structure and completeness can be enhanced.

IntroductionAre the research questions/hypotheses/predictions clearly presented? [ ] Yes,

Does the introduction build on relevant research in the field? [ ] Yes, but the research can be framed better in current knowledge, now the introduction is nic ebut broad

Materials and methodsAre the methods and analyses sufficiently detailed to allow replication by other researchers? [ ] Yes, but structure and clarity can be enhanced.

Are the methods and statistical analyses appropriate and well described? [ ] Yes, but structure and clarity can be enhanced.

ResultsIn the case of negative results, is there a statistical power analysis (or an adequate Bayesian analysis or equivalence testing)? [ ] I don't know

Are the results described and interpreted correctly? [ ] No, some conclusions are too general and should be more detailed explained

DiscussionHave the authors appropriately emphasized the strengths and limitations of their study/theory/methods/argument? [ ] No, limitations, especially on how the role of food can be disentagled from that of risk, should be more carefully and better explained

Are the conclusions adequately supported by the results (without overstating the implications of the findings)? No, has to be imporived

Download the review

Strengths: the authors have clearly done a lot of different work tackling the problem. The overarching goal to link animal behavior to ecosystem characteristics is ambitious and important, and several specific ideas and interpretations are interesting.

Weaknesses: I think the manuscript would be much stronger with a narrower focus aiming to answer more specific questions. The introduction is too general and broad to get a strong sense of what the authors intend to do. The discussion does an admirable job trying to tie the evidence together, but I wasn't entirely convinced by many of the arguments. Part of this may be the unavoidable circularity in causal effect that the study seeks to answer, between both deer and plant (deer both depend upon food and directly manipulate their food resources by eating), and deer and whatever hunts them. I think the inference and interpretation here would be stronger with a time-series or more formal before-after types of interventions. I recognize that this is not data the authors can easily collect, but I believe it would behoove them to think closely about the questions they can answer well.

A key evidential weakness or missed point of discussion is the potential effect of numerical drivers across these patterns. Yes, the islands will have different risk legacies, but also different deer densities that vary over time in different ways (and perhaps different environmental contexts), and deer density likely both shapes certain aspects of deer behavior (this goes back to Fretwell and Lucas) but can also lead to different patterns irrespective of behavioral differences. More or less deer can lead to certain outcomes independent of risk-response.

Finally, one of the challenges in trying to link behaviors to broader ecosystem characteristics or processes is that one must contend with a large conceptual and empirical literature (both the ecology of fear and trophic cascades feature a huge literature with many important conceptual papers). As it stands, I didn't think the authors laid a very convincing conceptual foundation for how the proposed mechanisms would lead to the observed patterns. As an example, although the strongest point of comparison relates to locations with varying degrees of human related risk (vs. risk from non-human predators), the authors don't take into consideration the hunting mode and process of humans (which plays a key role in how deer should respond). Instead, they seem to attribute this to the shoreline hunting of wolves as a driver of deer shifts away from the coast under predation pressure. This seems misaligned with the actual contrast that is reasonably tested here. Moreover, the justification for this thinking seems to be that deer should avoid open areas if facing cursorial risk, which both largely depends on the tactics deer actually employ to avoid risk (e.g., vigilance?), and frankly confusing in that the papers noting that wolves hunt shorelines focus on salmon and sea otters, which wolves are probably not hunting in a cursorial style.

In short, I had the feeling it would be good for the authors to dig deeper into the literature and think through things more carefully.

Line comments below:

General: I'm concerned that certain terms are being conflated throughout the manuscript. Risk is risk, fear is perception of risk, and any subsequent behavioral response arises from trade-offs between fear (not risk itself) and other competing considerations. E.g., on L291, most theory would predict that deer use of any habitat is "shaped by both fear and forage".

L69: I'd add the Gaynor et al. TREE paper as a citation here.

L70: I think this is a little too simplistic. It's not just the presence of risk, but the degree to which prey perceive (or anticipate, or react to) risk, the degree to which changing behavior can reduce that risk, and the counter-costs

of undertaking a behavioral change. A starving animal may not reduce foraging. An animal may not necessarily change where or when it forages if these provide no net benefit. Etc.

L96: I think one might generally anticipate that deer behavior varies to some extent (and for several possible reasons) across islands. To me, specific predictions (i.e., how one expects deer behavior to vary given the hypothesized mechanisms) would be more compelling.

L127: If possible, it would be nice to see some sort of density estimates for each island (if available) in the table. The authors might also use treatment codes for each island rather than their actual names (as they generally do in the results).

L166: I'd reword this. ("associated with" vs. "shaped by"). I'd presume vegetation cover is partially shaped by the accumulated patterns of risk (over potentially long periods of time; so maybe "risk history" is better than "risk"), but also by many other factors.

L180-191: not sure it makes sense to present this briefly here and then again in more detail in the next section. Suggest condensing.

L193: hypothesize rather than conclude? To be honest, I had some difficulty with this hypothesis. I would believe tidal areas with open sightlines might be riskier from the perspective of human hunters, but not convinced that the natural predators (which can only kill deer at very close range) are necessarily more dangerous in more open locations than forests.

L202: Is the environmental setting for this experiment consistent? I can imagine, for example, that an observer might not detect a deer (or be detected by a deer) at closer distance in a forest vs. some other context.

L640: Can one distinguish variation in risk from variation in density, or are these utterly confounded?

L717: Yes, deer can pretty easily take a bite and look around while chewing.

L723: I think it's very difficult to say that this is a selection pressure vs. a behavioral shift—and these are distinct mechanisms.

L753: Perhaps, but it depends on how deer manage risk. If they predominantly use vigilance to do so, then open habitats may be safer. Moreover, the key predation pressure that is reasonably tested in the study is human hunting—is this cursorial?

L793: Sure, but those wolves are primarily using those areas to hunt salmon or sea otters or other food items. It's probably clear by now, but I don't find this argument terribly convincing.

Reviewed by **Thomas Guillemaud** 🆔, 04 March 2024

Report of data and script editor:

After several exchanges with the authors we could reach a point where all the questions below are replied by a YES.

My final instructions to the authors were the following:

-in isotope deer new 2021.R, it would be good to warn the reader about the time needed to run the MCMCs (at least on their computer).

-In all scripts, be sure to have the comments in English (not in French)

-Make a true Zenodo deposit (not just a sandbox version), with a proper date deposit, get the doi and indicate it in the next version of the manuscript if it goes in revision

1- Can we get the data and script from the links indicated in the submission form or from the article itself? Yes
   2- Is there a readme file. Yes
   3- Are there metadata for the data and comments for the scripts? Yes
   4- Are the readme, and data files understandable by a normal reader? Yes
   5- Do the scripts run on the data? Yes
   6- Are the results the same as in the paper? Yes