From fear to food: predation risk shapes deer behaviour, their resources and forest vegetation

Martin et al.

Response to general comments of Gloriana Chaverri

Q1: *Structure and clarity need to be improved throughout.*

Q2: *Some of the arguments in the discussion are not convincing or are highly speculative*

Q3: *Conceptual framework needs strengthening.*

Q4: *Dig deeper into the literature and think through things more carefully*

> **R to Q1-Q4** We took good note of these comments. We addressed Q1 and Q2 to our best and hope the response to below the specific comments will reflect it.
>
> **RQ4** Point well taken. Further literature search did not provide major relevant ancient literature beyond what we already had in our collection but lead to very relevant publications that came out since our initial submission. Where appropriate during the revision, we used the latter in addition of more papers we already had. The treatment of specific comments helped clarify several points and make the conceptual framework more explicit. The revision should be more informative to a reader not specialized in the field which, we concur, was a problem to fix in some parts.

Q5*: Comments and suggestions in attached pdf.*

> **RQ5** These were extremely useful and will be addressed item by item below.

Q6: *Lacks hypotheses and/or predictions that would allow the reader to critically assess your results on the basis of evidence from previous studies.*

> **RQ6 OK:** We revised the introduction with this comment in mind. See in particular line 113 - 123 about predictions. We made sure evidence from other studies were explicitly provided and complemented them where necessary.

Q7: *You should at least have a hypothesis for each major section. 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 behaviours 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 behaviour, 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.*

> **RQ7:** We feel this is dealt with in lines 113 to 128

Q8: *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.*

> **RQ8:** We revised the result section and reduced the word count by 20%. We reduced the number of Tables from 7 to 4. The number of figures has not changed but figures were revised according to suggestions. We removed unnecessary details in text to highlight key results. We did not add a supplementary material section but chose to retain only the most relevant material.

Q9: *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.*

> **RQ9:** Good point. We provided a clear prediction. We included in the PCA the data from the islands without deer, initially only present in the graphical representation of vegetation profiles. In the latter we followed your suggestion and produced a new Fig. 3, indeed a significant improvement! This prompted a revision of the result section that addressed your other suggestions (see below).

Q10*: You add raw results to the main text and I suggest you remove those data and include in a table (perhaps even as supplementary material).*

> **RQ10:** OK. The revision got rid of the data in text and data retained was included in figures.

Q11: *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 not overly convincing and I have seen many other ways to quantify differences in communities among sites that are not included in this study.*

> **RQ11:** Good suggestion. We agree that this section lacked details. It has been revised in the text on predictions, in methods, figures and results (see in particular lines 377-396) which have been thoroughly revised. The use of beta-diversity was a misnomer. We focused exclusively on % cover in the understory below 1.5m. The data was collected on individual species subsequently pooled into several key plant groups. We had dealt with alpha and beta diversity in this set of data in separate publications (references are provided). Here we limit the analysis to cover as we feel this delivers the message. Species composition is only addressed through the relative proportions of cover of the plant groups in the understories. The point about smaller plants, you rightly emphasized, is addressed now in the discussion based on extensive work we published showing that almost zero % cover perceived by the observer does not mean zero food for deer. It means a different provision of food via a flux of emerging vegetation and

canopy fall of leaves almost instantly consumed by deer and only measurable through experiments (small exclosures) and direct observations of foraging deer.

***Q12**: Section "Did (the absence of) risk affect the use of exposed habitats?", where you seem to connect deer behaviour 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 behaviours was not significantly affected by the presence of abundant and higher quality forage". Again, your data do not provide any support for this.*

RQ12: OK, the text led to some confusion. The abundance of forage mentioned here referred to the abundance of forage in the adjacent forest not in the exposed intertidal. The reasoning is that an abundance of forage in the forest understory could alternatively explain why deer use less the intertidal. We tried to clarify this. See lines 129-140 in introduction, lines 335 and following about the approach, lines 609 and following for a clarification of results and their significance and lines 741-764 in discussion which has been significantly revised. We agree that because deer, predators and vegetation are tightly linked, teasing them a part is difficult. It may actually be futile at some point, the challenge being precisely to understand how they are intimately related. In the section on use of exposed habitat it becomes rather tricky. We hope that the rewrite and better prediction, plus better use of the lessons from the literature, now allows a more convincing argument, an argument that by no means intends to provide a black and white conclusion.

***Q13:** I think you are presenting your results a bit backwards. For example, it seems that changes in behaviour 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.*

RQ13: As pointed out by one reviewer there is some circularity in the system with a constant feed-back in the relation between deer and their environment, a relation that varies in dynamics under different risk contexts. The order we chose is, in some ways, related to the history of that interaction on Haida Gwaii. First there were no deer, then der were introduced in a "world" without predators and they progressively changed the vegetation landscape, that change affected their access to food without preventing high population densities. This, in the absence of risk, had consequences on their behaviour. Finally, culls in some populations, reversed trends in the vegetation and were associated with shifts in deer behaviours and possibly in habitat selection. The order we adopted was also closer to how the story unfolded for us over the years (almost 30!) with first questions raised by the contrasts in vegetation between islands with and without deer and little by little associated to questions on deer, how they deal with the change they cause and how to explain the contrasts in behaviour we observed when fear is brought into the picture. We hope that in the revision we corrected the apparent contradiction between how the ideas are presented upfront and the order we treated the questions in the core of the manuscript.

Comments by Gloriana Chaverri in pdf

We incorporated all grammatical comments and typos

Line 37:

See the reorganization of the section on use of shorelines

Line 96: *suggestion to add hypotheses*:

Done e.g. see line 115 and following

Line 166: *another comment on hypotheses:*

Addressed in revision

Line 177: *rationale for ACP*:

See lines 221-231

Line 180:

Section has been reorganized as suggested in comments, see lines 232 and following.

Line 221 *you write "Although in the model you could have added a random variable (deer ID) and thus have a richer dataset while avoiding problems of pseudo-replication*"

See lines 253-256 in revision for a more accurate description. Once an individual was encountered on no-risk islands, it tended to stay close by and has been tested repeatedly by some observers during an encounter. In these cases, we retained only the first event of the encounter.

Line 229: *why log transformation:*

To ensure normality of the data, line 270-272 in revision.

Line 256: *formula on rate of visits*

Done, actually this part on the rate of visits has been deleted as unnecessary in the demonstration.

Line 258: "please explain"

Done, see line 301-302.

Line 262: "bait friendliness"

Done, meaning explained line 304-305.

Line 291: "*You explain in detail the process to establish isotopic signatures, but it is not clear why all this information can be used to test the link between shoreline use and fear to predators. I think you should explain your predictions, providing evidence that populations that experience high predation risk typically avoid shorelines."*

See changes in lines 129-140 and 335-346.

Line 253: "*How does Figure 2 allow me to reach this conclusion? The graph tells me the difference in the coverage of plant groups per site (e.g., ferns, grasses and conifers are more common in Reef>1997), but not that in general the sites with a history of hunting had low cover. Maybe my confusion just arises from not understanding entirely how you ran the PCA and what each PC is measuring. For example, is PC2 measuring % cover, primarily of conifers and grasses, secondarily of ferns? I think you need to explain in more detail what this graph is showing here in the text*."

The description of fig. 2 and edited fig. 3 have been thoroughly revised to address this point (lines 375-395).

Line 358*: Meaning of PCA components?*

Meaning of PCA components is now explicitly define on fig. 3 and in text line 376-395.

Line 382*: Suggestion on Figure 3*:

Done, Fig. 3 has been revised according to suggestion.

Line 391: "*You should summarize all these behaviours in a single section. Your manuscript, and especially the results section, is very long, and creating extra sections when there is no need adds unnecessary confusion*."

Done, text has been regrouped in a single section as suggested, and shortened whenever felt possible. Starts line 412.

Line 402:

Done, as suggested Table 2 has been deleted and sample sizes included in figure, Table 3 and 4 have also been deleted.

Line 466*: written expression of stats*

Done, written expression of statistical results has been standardized…e.g. line 420.

Line 478: "*I would argue that this also could belong to a section on how predation history could affect overall behaviour of deer*."

Done.

Line 508: "*I think most of the information provided here is irrelevant. Please try to summarize into main findings. As I suggested above, your results section is very long, and having all these details makes it increasingly difficult to grasp the main findings. Another option is to include all these details (if you feel they are somehow relevant) into a supplementary text*."

We retained option one but reduced text (24 lines instead of 43 lines). We reorganized text to improve flow and digestibility. Lines 437 and following.

Line 532: "*My opinion is that this is not really adding much to the results. I think you have sufficient evidence from the other measures of behaviour*."

We kept the data but could reduce text from 11 lines to … three. See line 514-516

Line 549: "*I find this very interesting; however, it is not very clear how this contributes to the "story". Maybe once you provide predictions it will be clearer why changes in diel activity patterns are relevant in this context*."

OK. See lines 126 to 128 for description of why this is in the story.

Line 588: "*Is there any way to quantify these differences? To me these conclusions you are drawing seem to be based on just subjective observation of the figure, not objective quantification of results. Maybe I am wrong, of course, and the results of these mixing models are normally assessed in a different way. If the latter is true, then it would be good to have an explanation about how to best interpret the results based on previous studies*."

There is objective quantification, see now lines 541-545 and 554-559 and Fig. 8.

Line 616: "*This already provides interesting data that could help the reader understand the results of the section "Understory vegetation varied with risk history*".

Good point, we revised text to better do this, see lines 570-574 and 669-695.

Line 622: "remarkably"

Fixed!

Line 646: *beta diversity?*

Fixed: unfortunate use of "beta", deleted.

Line 712: *"What data is this observation based on?"*

It is based on the lack of change in behaviour in the deer moved from understory poor Kunga to understory-lush post-culls Reef. Revision of entire text intends to make the link clear, see lines 670-702.

Line 721: "On what data is this observation based on":

Now much more explicit in text, see lines 670-702 on the assumed link between behaviour change and forage availability.

Line 732: "*This seems highly speculative. Is there evidence, from your study or results of others of this? I think that once the results of your section on whether really the understory can be considered "intensively browsed" are clearer this will make a lot more sense*."

We hope the revisions on deer impact on the understory and discussion lines 670-711 clarifies why we propose this interpretation (also see response to next query).

Line 735: "I *do not understand this section. I do not believe it is adding any relevant information to your discussion*."

This section's title has been deleted and the point it was trying to address has been entirely readdressed in the revised text. The question is: can absence of risk help understand how deer can maintain high densities (30/km² as stated in introductory sections) despite what seems an understory devoid of vegetation. The answer suggested is: it is possible by giving up fear and associated behaviours to focus on resources that require more time to be collected, lines 670-711.

Lines 734, 756 and 760 *on speculation and interpretation on shoreline use:*

Point taken but see revised treatment of this section lines 748-762.

Line 784:

OK! But see lines 748-762.

Lines 801, 805 *long sentence and speculation:*

Done: long sentence has been shortened and entire section has been reorganized and revised. See lines 764-796 about speculation.

Response to reviewer 1

Q1: *I think the paper is not clearly structured and written which hampers bringing across the message. Therefore, I would advise to severely revise the text of this manuscript to enhance the clarity Major remark 1: Clarity/structure: The text is in many places not well structured and has an unsuitable use of paragraphs. The abstract lacks important information. Throughout, the text and structure of the papers should be enhanced. The methods and data analyses seem legit but it is difficult to assess with the text in this condition.*

> **RQ1:** The revision confirmed that the point made was valid. Our revision can be qualified as severe. We made extensive changes to the original text to improve clarity and flow of argument. We rewrote the Abstract and sections of the introduction. The changes we made in the made in "material and methods" section intend to improve pertinence and structure of "results" section.

Q2: *The introduction does not accurately situate the research within context and does not highlight research gaps. It provides a nice introduction to the ecology of fear but then quickly jumps to the current study, without obvious links.*

> **RQ2:** OK see revision in lines 71 – 90 and 90 – 98.

Q3: *Methods: Maybe it is good to give a general overview of all the island first. Overall structure could improve. A lot of data is collected in different projects, perhaps provide an overview and introduction to this. Also, the role of large predators is small in the methods. What are their densities, what is known on their behaviour and prey choice?*

> **RQ3:** For the point "general overview of the islands" see line 156-166. Overview on project: see lines 160-170 and revisions in introduction and method section that intend to improve grasp on the relationship among the different projects. On large predators see lines 110-113; 129-139 and 207 – 215.

Q4: *If you want to elucidate the role between forage availability and risk, is another, more appropriate analysis then possible?*

> **RQ4:** We are not entirely clear what is meant by "role" in the comment. If the meaning is link between forage availability and **risk,** then see our discussion on Kirchhoff and Person 2008 (see line 678 and following) and the following response to a query of reviewer 2. The modelling exercise of Kirchhoff (see reference Kirchhoff and Person 2008) shows you can have similar deer density and different vegetation cover in presence or absence of risk. We have shown that high deer density occurs in situations of low vegetation cover and no risk (Le Saout et al 2014 Wildlife Biology). Kirchhoff and Person's work argues that high deer density can be observed in situations of high veg cover and presence of wolves: "(…) *Simulation models that introduce wolves to Haida Gwaii indicate that a high-level equilibrium is likely*."
>
> If it actually means between forage availability and FEAR see lines 670-711 in discussion.
>
> *"Is another more appropriate analysis possible?":* We do not think that with the data at hand we could look differently at the links between risk and forage availability. We hope that the clarifications we made on the rationale, results and discussion better show the pertinence of our analysis.

Q5*: So many nice experiments and data! Please provide an overview at the start of the methods, and link each to a hypothesis and make clear in the results and discussion how you come to your conclusions.*

RQ5: See response to the recommender on this point (her Q1 and Q7). Hypotheses have been specified and structure of discussion adjusted accordingly, and lines 233-236 for an overview of the approaches used for behaviour.

Q6: *The discussion addressed many of my thoughts, but the structure and clarity can be improved, and moreover sometimes the conclusions are too broad, general and strong.*

RQ6: OK we agree. Revision of discussion ended up reorganizing the argument that was indeed sometimes going back and forth. About "broad and strong conclusions" see where specific items are addressed in specific comments.

Specific comments reviewer 1

L29: *"deer in risk-free population" is this grammatically correct?*

Fixed.

L42: *the mention of the 'intertidal zone' comes a bit out of nowhere. This could be described in the methods section of the abstract (which seems to be lacking).*

OK. See lines 28-31 in abstract, and 168-169.

L51-62: *Nice background. But if needed you could start closer to the topic by introducing (behaviourally mediated) predator-prey interactions; i.e. ecology of fear, as done in the second paragraph, and leave this first paragraph out.*

We are inclined to keep the first paragraph. See revised lines 74 and following for transition.

L67-69: *Landscapes of fear, and how they affect ecosystems could be more precisely explained.*

OK, see lines 73 -90.

L56: *typo: '['*

Now […]

L75-76: *I do not agree that it was (only) the increase in large herbivore populations that allowed predators such as wolves to recover, also land-use changes and legislation seem important to me, at least locally.*

Absolutely correct! See paragraph lines 98 -100 as revised. We totally agree, legislation played an essential role, especially in Europe, and allowed wolves to benefit from the recovery of their prey populations part because of land use changes and part because of changes in hunting regulation + active propagation by hunters in some species.

L81-82*: it seems to me that these undesirable impacts of herbivores should be either mentioned and exemplified, or not.*

See line 93-98 as revised. Still short but hopefully more to the point.

L86: *what do you mean with 'effects of high deer abundance'. Maybe introduce this beforehand?*

Good point we more accurately meant "deer effect on forest ecology" see now lines 102-104.

Methods

L106-L108: *most of the area is forest, but are there open patches? Intertidal? Describe here?*

OK see lines 144-148 and 163-170.

L177: *how was data normalized?*

Centered and standardized (line 228).

L182-183: *how were activity patterns measured? Not clear here, it is later on in L267-268.*

OK see line 233-236 introducing lines 310-319.

L196: *grammar: "…for by…"*

Fixed.

L217: *how often did deer move out of sight?*

Fixed: see lines 251-252.

L278*: I wonder if the fact that the selection of repeatedly trapped deer affects results, as they may have personalities different from those of the main population.*

Good point. Close to 60% of the deer trapped on Kunga were trapped at least 3 times, so we consider that the translocated deer were representative of bold personalities on Kunga (see fig. 5).

L280: *redundant [*

Fixed.

L291-359: *The paragraphs are not so well organized.*

Section has been reorganized see lines 738-762.

L640-644: *"these results illustrate" I find a bit bold and brief.*

We did not revise this paragraph but hope that edits in many other parts of the manuscript make clearer what this short statement summarizes.

L780-787: *does your data allow to elucidate between effects of forage or risk?*

OK, this comment clarifies the reviewer's earlier point. It does, to some extent, but the two factors necessarily interact and with an important role of time. We expanded and reorganized the discussion of these results and hope to convey a clearer message. See lines 757-762.

L801-802: *Did hunting lead to altered behaviour or to selection of individual's personalities? It is discussed in the following paragraph but not clear here.*

The sections were this is discussed have been quite heavily edited and reorganized which hopefully improved the flow and clarity. See e.g. lines 712-737. The argument is that hunting "selected" personalities more apt to elude hunters and more appt to behaviourally respond to the sudden threat.

Discussion has valid points but I find it a bit chaotic and unstructured and the effects of risk and resources are intertwined and cannot be really disentangled.

The reorganized discussion should have dealt with the chaos issue. For the risk versus resources point see comment above on this point.

***Abstract**: it is not entirely clear what was measured and which analyses were done. It would be good to mention this in the abstract.*

Abstract has been severely revised and we hope it fixes this point.

***Keywords**: can keywords be a combination of words?*

Some combinations have been simplified.

Response to reviewer 2

***Weaknesses:** I think the manuscript would be much stronger with a narrower focus aiming to answer more specific questions.*

Focus remains the same and is broad by essence, but paper revision is structured around questions that have been better specified.

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.

Introduction has been revised to better announce the objective of the work. Yes, true in part about the narrow connection between deer and plants.

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.

This study draws on over 30 years of investigation that documented many changes and documented before and after changes (e.g. what was seen for plants (and deer) before and after the culls). We feel there are questions we can answer well and questions where we can draw tentative conclusions that may open perspectives for research.

A key evidential weakness or missed point of discussion is the potential effect of numerical drivers across these patterns.

Such potential effects exist but are controlled as much as possible (see revision in introduction and material and methods about deer densities).

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 behaviour (this goes back to Fretwell and Lucas) but can also lead to different patterns irrespective of behavioural differences. More or less deer can lead to certain outcomes independent of risk-response.

Islands are comparable in terms of forest composition and state lines 163-168, and comparable in deer densities (see lines 160-170).

Note also that modelling exercise of Kirchhoff et al. (see reference Kirchhoff and Person 2008) shows that you can have high deer density in different contexts of vegetation cover depending on the presence or absence of risk in particular, high deer density can be observed in situations of high vegetation cover and in presence of wolves] "*Simulation models that introduce wolves to Haida Gwaii indicate that a high-level equilibrium is likely*." (Kirchhoff and Person 2013), but also, as we have shown, that high deer density occurred in situations of low vegetation cover in absence of risk (Le Saout et al 2014 Wildlife Biology)

Finally, one of the challenges in trying to link behaviours 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).

We hope that the revised text makes better justice to our conceptual foundations without too much expanding the text.

Hunting modes: True and we did not elaborate initially on hunting modes but are more specific in revision. We were indeed familiar with the literature on the subject. Lines 109-110; 129-140; 739-762; some aspects of this comment.

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.

Unfortunately, we cannot fully agree here. We admit that we did not elaborate much on the subject, and we feel it has been corrected (see line references in previous point). Shoreline hunting of wolves and its effect on deer use of shorelines has been demonstrated by Klein, and work has shown that, for deer, cover is perceived as more secure than openness (not necessarily the case in other herbivores). This is now specified and backed by text and references in the revisions. The studies on salmon or sea otter hunting also mention that, where these species can be alternative prey, deer densities can be driven to very low levels because of wolf predation. As for "cursorial risk" vigilance will allow to detect it, but flight is key in avoiding a lethal outcome.

As for human hunting as now mentioned in revision, it is often taking place through access from the ocean, as many areas involved in the study are roadless.

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.

> Maybe this was not well highlighted in the first version of our manuscript, but the authors are highly aware of the literature on this subject. See "Martin J-L, Chamaillé-Jammes S, Waller DM. 2020. Deer, wolves, and people: costs, benefits and challenges of living together. Biological Reviews **93**:782–801. » We hope the revisions in the introduction and discussion sections make this clearer.

General: *I'm concerned that certain terms are being conflated throughout the manuscript. Risk is risk, fear is perception of risk, and any subsequent behavioural 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".*

> OK, the point is trying to understand how the two interact and under which circumstances

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

> Done.

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 behaviour can reduce that risk, and the counter-costs of undertaking a behavioural 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.*

> True, and this is mentioned in text. We have shown and references are given in text that there is no shortage of forage but a radical change in how that resource occurs in the understory which could affect costs in acquiring that resource. We assume (with documented arguments) that none of the studied populations are food limited (see Le Saout et al 2014 in Wildlife Biology).

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

> Agreed on predictions: More specific predictions are provided in the revised manuscript.
>
> Within the no-risk category we have shown (see the references provided) that ecological conditions, overall deer behaviour, and deer densities are remarkably similar and this is actually documented by results presented here both for vegetation and deer behaviour.

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).*

> Done, in text not in table lines 160-170, 197-199, and 204-206.

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.*

Rewording done.

Accumulated pattern of risk: correct, risk history makes then sense.

Many other factors: sure, but conditions were controlled as much as possible.

Note that on no-risk islands deer became the overarching ecological factor, see number of our studies on Haida Gwaii, among others Chollet et al. (2021), even on Graham island, where it was shown that the expression of all other ecological factors was "overridden" by deer (Chollet et al. 2021 Annals of Botany – in references of manuscript).

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

Section has been reorganized.

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.*

Correct for humans, but evidence at hand suggests that it is also the case for wolves
See lines 129-132. "hypothesize": text amended.

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.*

Yes it is consistent, observations were made in forest habitat.

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

When it comes to patterns of the understory vegetation all No-risk islands have comparable deer densities based on the data and studies available, on Reef densities are still lower than pre-cull densities and the vegetation pattern results essentially from the temporary but dramatic reduction in deer density. On Graham densities are comparable to those on Reef post culls at the time of study. On the BC Central coast, no solid data on densities are available but as shown by Kirchhoff and Person high densities are expected in presence of wolves and a dense understory.

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 behavioural shift—and these are distinct mechanisms.*

We understand a behavioural shift as a rapid change in behaviour in an individual exposed to a current threat. We understand a shift in the behavioural profile of a population as a change in the type of personalities that dominate in the population

following the differential selection of different personalities by some external perturbation (here the culls), a change that would be retained in the population several generations after the perturbation in an isolated population, assuming that differences in personalities are heritable. We tried to reword the discussion to make this clear.

L753: *Perhaps, but it depends on how deer manage risk. If they predominantly use vigilance to do so, then open habitats may be safer.*

We tested costly antipredator behaviour namely flight or habitat avoidance, vigilance has no cost and is not affected by risk as we have shown (*Chamaillé-Jammes, S., Malcuit, H., Le Saout, S., & Martin, J.-L. (2014). Innate threat-sensitive foraging Black-tailed deer remain more fearful of wolf than of the less dangerous black bear even after 100 years of wolf absence. Oecologia, 174(4), 1151–1158*.)

Furthermore (lines 88-93) studies suggest that, for deer, open habitats are perceived as riskier and e.g. Klein 1995 shows that on islands with high wolf predation risk deer have retreated into forests and steeper areas away from the shorelines.

Moreover, the key predation pressure that is reasonably tested in the study is human hunting—is this cursorial?

No, and we do not assume them as cursorial. But this does not affect the part on use of shorelines (see lines 129-140). The specificity of human hunting, which is by day light, intervenes in the study on risk effect on diel activity.

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.*

We feel this argument misinterprets the literature on the subject as mentioned in previous points we tried to alleviate this misinterpretation in the revision of the text by being more explicit.

Review by Thomas Guillemaud, 04 Mar 2024 07:06
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