Decision

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Optimal foraging in a changing world: old questions, new perspectives

The preprint entitled "How optimal foragers should respond to habitat changes? On the consequences of habitat conversion" has been reviewed by two experts in the field. Their opinion largely converged, and I subscribe to their recommendations. This manuscript revisits the classical foraging problem of "marginal value theorem" (MVT). It addresses a question which could appear at first sight as only a minor development of previous works by the same group. Yet, since it is a non-trivial task to a priori predict the direction of changes in the residence time as a function of the modification of the frequency of habitat qualities, I consider that this question deserved a rigorous investigation. The present study could therefore be a valuable contribution to the field and it could be recommended by PCI-Ecology provided some clarifications and developments.

In its present form, one the major weaknesses of the manuscript lies in the presentation of its aims and goals, particularly for a general audience readership not familiar with the recent theoretical developments about the MVT. I strongly recommend a more thorough presentation of the ecological context in order to help the reader to appreciate the biological relevance of the theoretical choices presented herein. One possibility would be to provide several concrete ecological interpretations of the habitat changes, either in the introduction or the discussion section, or both. What could be the practical implications of these results in the field?

-> In the revised version we have increased the connections to ecological reality, e.g. in the Introduction, and brought in novel literature references. Most importantly, we have added an entirely new Figure (Fig. 4) that presents numerical (simulated) temporal dynamics and we think this should help readers "visualize" what our results mean in practice. A major improvement is also the explicit comparison of optimal and non-plastic foragers, that provides new predictions and ways to confront data and theory. All this, plus a general effort to render the Figures and the text less theory- and more ecology-oriented, in our opinion makes the paper much more accessible.

I also share the referees' opinion that the preprint can be improved in numerous points of details, in the presentation of either the equations or the results. Each point taken separately is not such a hurdle, but collectively they hamper the understanding of the study. For instance, the presentation of the rationale and the interpretation of the dummy variable x (line 113) deserves greater care to help its understanding by an ecologist readership.

--> We have addressed the various specific points raised by the reviewers (see point-by-point responses below), and we'd like to thank them for their thorough reading and recommendations. We agree that the meaning of x is an important point and we hope it is now clearer throughout (see response to reviewer 1 and lines 108-110, or lines 119-120).

Fig. 2 is important but confusing. The MVT is a classical question in behavioural ecology courses because it can be introduced as a geometrical model, with a minimal amount of equations. In the canonical presentation of the MVT, the beauty of this model (from a teaching point of view) lies in its graphical resolution by figuring the average travel time between patches as a negative point on the x-axis and plotting the line which crosses this point and is tangential to the energy gain curve. It is fairly intuitive that this point of tangency is the optimal residence time in the patch because it maximises the rate of energy gain (energy divided by the travel and residence time). In fig. 2, the dotted lines obviously correspond to such tangent lines, but strangely enough they appear to be parallel, which corresponds to different travel times between patches. It is thus hard to interpret the

difference in within-habitat correlation.

→ Regarding the tangent line going though -T (see also our response to Reviewer 2 below), this graphical construct is only valid in homogeneous habitats (all patches identical). But in the general (several patch-types) case there is no such construct: the optimal residence times are such that all gain functions are tangent to *SOME* tangent line (of slope En*), but there is no graphical way to compute En*. This is explained in the different references cited in the article. That is is why the lines are indeed parallel, and why we do not show -T: obviously our habitat conversion scenario requires considering heterogeneous habitats. This also motivates, in part, our claim that "usual graphical arguments" used with the MVT are of little help to address the questions tackled in this MS (lines 24-25), and makes maths more necessary.

That said, Figure 2 has been entirely redrawn. We now provide three (not just two) examples, and give the explicit gain function that was used to generate the different cases. Since this is the most classical gain function used in the literature, this should help the readers. Furthermore, the legends and explanations in the main text have been seriously enriched. In particular, we use an explicit notation (\rho_INTRA) to describe the within-habitat correlation (a notation already used in an in-press paper) and call it the "patch exploitation pattern" throughout. It is now at the center of our Results (and is mentioned in the Abstract).

More generally, the modifications suggested by the referees will surely improve the readability of this manuscript, and ultimately its understanding by non-theoretician ecologists.

→ We agree and thank them again. The different revisions not only improved the readability of the manuscript but also prompted us to uncover novel predictions/results.

REV1

This paper addresses an interesting question -- how mean residence time in patches depends in the distribution of patch quality, perhaps due to some sort of habitat conversion. I'm not sure whether it is mainly because of this particular publication venue, but I found the paper difficult to evaluate because of the extensive referencing of earlier and closely related work by the same authors (for example, in the paragraphs that follow Figure 1 on page 2). The same is true of the Conclusions, which focus on showing that this approach is "equivalent" to the earlier work, although in a sense that is not fully clear to me. The overall framework seems to me to be sufficiently familiar and clear to be able to stand on its own with the more usual reference to earlier work.
As a related issue, the motivation presented feels like "let's see what happens if we extend our earlier model" (for example at the bottom of page 2). The general point about travel frequency could be emphasized. In fact, why not be more explicit about the importance of movement rates due to habitat conversion, perhaps by looking at a very simple model of a pollinator? Another possible application would be as a way to investigate some of the effects of competition. The distribution of patch qualities would also change if competition for resources, or renewal rates of those resources, were to change. This could provide a simple mechanism for altering the underlying parameter x that controls the distribution.
--> Thank you very much for the review. We have rewritten the abstract/intro/Discussion and included several additional references, so that the article is now focused on presenting our new results and predictions. Comparisons with earlier works have been tuned down importantly and have become more peripheral statements. We believe the revised ms now stands on its own.

The only technical issue that concerns me is the exclusion of unexploited patches. The set of exploited patches depends on the realized fitness value En^* and will thus change with the overall distribution of patches. In my experience with models of this type, there isn't an easy way to deal with this issue up-front. I think this could make some of the derivations rather more complicated. This issue is more difficult to address when the gain curve is sigmoidal rather than concave down, where excluded patches can be recognized directly from the slope at $t=0$.
--> Our sensitivity analysis approach, by looking at infinitesimal changes in habitat properties (here, patch frequencies), simplifies the matter greatly as we can treat the set of exploited patches as a constant. Indeed it does not require computing the residence times or the set of exploited patches (which, we agree, can be a difficult task), but rather assumes a given solution and sees in which direction it changes when slightly perturbed. Generically, slight changes do not change the set of exploited patches, except in the improbable circumstance that one patch-type is exactly on the boundary of the set. When this occurs it would introduce some discontinuities if we were to integrate our criteria over sustained changes (one should then update the set of patches accordingly): the process would be well-posed, but in a piecewise manner. Otherwise it does not affect the results. This is one major advantage of the approach. We have added a paragraph on page 6, lines 147-152, to explain these aspects.

I also wonder whether the derivations would be more or less identical, although perhaps simpler, if patch types were drawn from a continuous distribution. This would show that the analysis here, of changing the probabilities, and the previous analysis, of changing the qualities, are *really part of a larger whole, where the probability density function itself is changed. Identifying the key statistics of that pdf would*

perhaps give a unified approach to the general problem.
----> This is an interesting suggestion, and one that we had pondered. It certainly seems quite elegant, but in practice it might be much less tractable. First, having a continuum of patch qualities implies that we cannot consider the simple homogeneous case (the latter is the limit of a Dirac density). We have the same issue in the present article, where we have to consider heterogeneous habitats (though with a discrete number of types). Compared to our earlier approach this already makes analysis less tractable. Having a continuum would add a further complication: we could not assume that any change in habitat quality leaves the set of exploited patches unchanged (see our response to your earlier question). Thus we'd have to track continuously what is the poorest patch worthy to be exploited. Second, changing locally the density of a given patch type would have zero impact on the optimal strategies (since any patch type has zero probability density) and would disrupt the continuity of the PDF. Thus we would need to specify an entire perturbation function with suitable properties and integrate it. Not to mention that habitat conversion is usually conceptualized with discrete patch categories (e.g. perturbed/unperturbed) rather than a continuum. Altogether, we agree this may conceptually bridge the two approaches, but we think it would be more involved mathematically, and we'd rather keep it for future developments.

I found Figure 2 about positive and negative correlations of resource
intake with residence time a bit confusing. Wouldn't this depend on the
value of En*? And is there a simple family of curves which can show the
full range of behaviors as an example?
--> We have added one panel in this Figure and we now explain much more throughout how to interpret the Figure in relation to En*. A simple family of gain functions was used to generate all the curves, and this is now indicated in the legend of the Figure (page 4; line 103).

On page 5, I found it peculiar to mention that the previous
varying a single p is internally inconsistent. If there is
include a simpler example before the more full analysis, it
more sense to increase one of the p's, and decrease all the
the fraction needed to maintain the constant sum.
--> We have addressed this point in the revised manuscript (p4 lines 83-84 and p5; line 103).

The goal of the calculation on page 6 is unclear, and I got rather lost
in working through the equations. The derivation of the first equation
on this page just by reference to earlier work was a bit frustrating
also.
--> The calculations (now on page 5) have been made more straightforward and lighter, with more textual explanations.

Figure 3 does a good job of illustrating the key results. However,
It didn't seem to me like region C was discussed in the rest of the
paper.
--> Figure 3 has been much enriched, and all regions are now discussed explicitly in the text.

3.2 line 113: It might be illuminating to give examples of what the
"dummy habitat variable x" could represent, when it is first introduced.
3.2 line 123-124: Criterion (6) comes from seeing x as a "metric of
habitat quality" iff dEn*/dx > 0. So the authors are specifying a
habitat variable where increasing x increases En* too (by changing
frequency distribution of patches). But couldn't there be a habitat
variable we care about where decreasing x increases En*? That might
still say something about habitat quality. I'm not sure why we want to
ignore it.
---> x is now defined precisely when first introduced, as the "habitat conversion pattern" (i.e. which patch types are converted into which; page 5; lines 108-109). It really is a dummy variable introduced for mathematical convenience, allowing us to write derivatives rather than infinitesimal changes (the latter notation being common in physics, but less so in our own biomathematical

background). It does not place any restriction on the set of possibilities, and has no specific ecological meaning.

For this reason we now call it a "dummy variable" and not a "dummy habitat variable" as we used to. Indeed it has nothing to do with a habitat characteristic.

Also, it can describe anything, and needs not increase E_n^*. It is simply useful to distinguish those patterns of habitat conversion that would result in higher fitness, from those that would decrease fitness. We hope our reformulations now clarify these aspects (lines 119-125).

3.3 line 133: I would have liked "average rate of movement" to be defined, rather than referring to an earlier work and stating it is inversely related to average residence time. But if this is a common term in the literature, maybe that is unnecessary.

→ We added a paragraph and two novel references to define the average rate of movement (page 6; lines 154-162)

3.3: I didn't feel that these results focused on the average rate of movement, even though this section was called that. In line 145, the authors mention that expression (7) is similar to (6) with a term added, which makes it sound like a mathematical similarity. I think it is rather a conceptual similarity, because in one En* is increasing with respect to x, and in the other t_j* is increasing with respect to x as summarized in lines 166-167.

→ We hope our rewritten Section now makes it clearer that the focus is on predicting the response of movement rate with x. The paragraph mentioned in this Section (ll 174-177) only compares predictions with the ones obtained above regarding the variation of fitness with x, as the ultimate goal is to compare the two, and thus to obtain predictions about the covariation of fitness and movement rate following habitat conversion.

REV 2

This manuscript reports the predictions of an extension to the marginal value theorem (MVT) model focussing on the distribution of patch quality in the environment. As the authors point out, models of the MVT typically focus on a single patch type, or a constant distribution of patch quality. It is important to understand how a change in the distribution of patch types may affect animal behaviour and fitness. One application that the authors highlight is in conservation, because anthropogenic degradation of habitats tends to be inconsistent, so increasing the proportion of patches that are poor quality, rather than reducing the mean quality of all patches. The authors take a very abstract approach, and whilst this provides some important general principles, the manuscript is probably of limited use to the general reader. Below, I highlight some potential improvements and some places where I found the working difficult to follow. I also suggest some revisions to the text and possible additional figures to aid intuition.

The abstract is rather short on results from the present paper, instead summarising the results of the previous paper in the series. The main insight (Figure 3) is not mentioned. The sentence starting "One expects" is not necessary, at least.

→ We have significantly rewritten the Abstract along the lines suggested by the reviewer. We have removed the unnecessary sentence.

Line 2: The citations are not ordered numerically.

→ Fixed.

5: Here and elsewhere, the phrasing is in the active voice ("is to change") rather than the passive voice ("is a change"), which suggests that a researcher is making the modifications in an experiment. I think the model is relevant to all changes, and the authors give an example of habitat degradation, so the passive voice would be preferable.

14: What is closed habitat? Good quality?

→ Closed is here intended as the opposite of open, i.e. with a forest cover (woodland), as often intended in this context. It might be considered as "good quality" for most foragers indeed, though some specialists might on the contrary prefer open habitat portions, so we do not decide whether it is good or bad (the gain function used in particular applications would encapsulate the decision).

17: I find the term "habitat conversion" rather confusing; it implies the whole habitat is altered. Perhaps "local alterations" would be better?

→ Considering that indeed the whole habitat is altered (in the sense that a significant fraction of, or even the majority of patches, can be changed, and that all patch exploitation times do vary), we'd rather stick to the classical term habitat conversion (that will also help readers identify the topic and relevant related papers). "Local alterations" could further suggest we are looking a a few specific patches in an otherwise constant habitat, which is suitable for a large range of MVT studies (e.g. GUD theory), but not for ours (in our case, the habitat cannot be considered as constant as precisely, En* (a habitat-level property) varies and feedbacks on patch-all exploitation strategies, and this is what causes most non-trivial predictions.

22: This claim needs an explanation or a citation.

→ We now provide a practical illustration of this claim in Figure 1: we reference the Figure (l. 25) and in the legend we explain the claim. Since the updated Figure 1 now has explicit graphical MVT calculations shown, it should be obvious that predicting graphically how the mean residence time varies is not possible.

25: /i and /j are undefined.

→ i is defined on line 54 and j on line 60.

41: Change to "previous negative effect of a change in foraging behaviour"

→ DONE

47: "For consistency" with what?

56: I would find it much clearer if the sum over j were in equation (1), rather than on line 60. Also, is the (t_i) necessary, given that we are differentiating w.r.t. t_i?

59: Is "effectively" necessary?

63: Move "thus...leaves it" to the end of line 66.

71: Is there an assumption that /Omega does not depend on p? If good patches become sufficiently rate, won't foragers add poorer patches to their exploited set (under at least some conditions)?

81: Can you add some intuition for the derivation of this? e.g. where do the _i come from?

89: "remark that"? 152: "remark that"?
90: What is the intuitive consequence of this?

91: I found the discussion about the two scenarios confusing. Good patches are those with high F/t and it seems odd to separate these terms. Whether good patches have low or high t* depends on the rest of the patches: good patches may have large t* if F* is also large or T is large.

Figure 2: An intuition for this difference is that 2a shows a case where patches differ in how easy it is to find prey but have equal densities, whereas 2b shows a case where patches differ in prey density. What might cause the curves to be non-monotonic? The best patch should be shown thicker or dashed, rather than a different dark colour. What do the dotted lines indicate? Would it be helpful to show tangents from -T?

115: Should this be "change in E_n"? What does "total variation" mean?

116: I don't follow this. Surely t* alters when x alters? Does what follows assume that the forager does not respond to the change in p_i, but uses a suboptimal strategy?

→ No, but it turns out (at first mathematical order) that the contribution of all the dt*/dx cancels out, and this is shown in details in the cited reference ([4]). This is now discussed in greater length since we explicitly consider the case of non-plastic foragers (what you call suboptimal foragers) in the revised version (see lines 133-138).

117: I found it very difficult to work out how this is derived.

→ The cited reference [4] contains the full length derivations. Here we decided not to increase the number of equations and derivation steps, considering this is not the core of the paper (and that the derivation has been published elsewhere).

120: What does "variation" mean?

→ See above: it is a calculus term for "change".

123: Does "metric" mean "positively relate to"?

→ Indeed

136: See where?139: See where?

→ This has been fixed.

139-141: I did not follow the derivation of this.

-> This Section has been rewritten with a larger part of calculations put in the Appendix. We believe this makes it easier to follow.

148: What is the insight from this?

→ In the revised version, the insight this gives is explained in much greater details (it helps understand the connection between patch-exploitation patterns and the effects of habitat conversion)

Figure 3: The axes seem very abstract. The general reader would be greatly helped by a figure that showed how En and t* change in response to p or x at certain points (e.g. 1 value of x-axis, 3 values of y-axis) for some representative functions.

→ Representative functions are now given (e.g. added in Figure 1) and a numerical illustration of temporal dynamics is provided (new Figure 4). The legend of Figure 3, as well as a new paragraph in the main text (lines 190-196) should make it much clearer what the axes of the Figure represent.

169: "curved enough"? What does this mean precisely?

→ This means that the mathematical curvature of the gain functions (precisely, the quantity H in the equations) should be strong enough, and this happens to coincide with the geometrical/intuitive interpretation of the term (the curves must be much "bent" or "curved", i.e. non-linear, "concave"). We have reformulated (lines 209-211).