Peer Community In
Ecology

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

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Frederick Adler, ***Andrew Higginson*** *and 1 anonymous reviewer*

Vincent Calcagno, Frederic Hamelin, Ludovic Mailleret, Frederic Grognard (2018) How optimal foragers should respond to habitat changes? On the consequences of habitat conversion. Missing preprint_server, ver. Missing article_version, peer-reviewed and recommended by Peer Community in Ecology. 10.1101/273557

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Marginal value theorem (MVT) is an archetypal model discussed in every behavioural ecology textbook. Its popularity is largely explained but the fact that it is possible to solve it graphically (at least in its simplest form) with the minimal amount of equations, which is a sensible strategy for an introductory course in behavioural ecology [1]. Apart from this heuristic value, one may be tempted to disregard it as a naive toy model. After a burst of interest in the 70's and the 80's, the once vivid literature about optimal foraging theory (OFT) has lost its momentum [2]. Yet, OFT and MVT have remained an active field of research in the parasitoidologists community, mostly because the sampling strategy of a parasitoid in patches of hosts and its resulting fitness gain are straightforward to evaluate, which eases both experimental and theoretical investigations [3]. This preprint [4] is in line with the long-established literature on OFT. It follows two theoretical articles [5,6] in which Vincent Calcagno and co-authors assessed the effect of changes in the environmental conditions on optimal foraging strategy. This time, they did not modify the shape of the gain function (describing the diminishing return of the cumulative intake as a function of the residency time in a patch) but the relative frequencies of good and bad patches. At first sight, that sounds like a minor modification of their earlier models. Actually, even the authors initially were fooled by the similarities before spotting the pitfalls. Here, they genuinely point out the erroneous verbal prediction in their previous paper in which some non-trivial effects of the change in patch frequencies have been overlooked. The present study indeed provides a striking example of ecological fallacy, and more specifically of Simpson's paradox which occurs when the aggregation of subgroups modifies the apparent pattern at the scale of the entire population [7,8]. In the case of MVT under constraints of habitat conversion, the increase of the residency times in both bad and good patches can result in a decrease of the average residency time at the level of the population. This apparently counter-intuitive property can be observed, for instance, when the proportion of bad quality patches strongly increases, which increases the probability that the individual forages on theses quickly exploited patches, and thus decreases its average residency time on the long run. The authors thus put the model on the drawing board again. Proper assessment of the effect of change in the frequency of patch quality is more mathematically challenging than when one considers only changes in the shape of the gain function. The expected gain must be evaluated at the scale of the entire habitat instead of single patch. Overall, this study, which is based on a rigorous formalism, stands out as a warning against too rapid interpretations of theoretical outputs. It is not straightforward to generalize the predictions of previous models without careful evaluating their underlying hypotheses. The devil is in the details: some slight, seemingly minor, adjustments of the assumptions may have some major consequences. The authors discussed the general conditions leading to changes in residency times or movement rates. Yet, it is worth pointing out again that it would be a mistake to blindly consider these theoretical results as forecasts for the foragers' behaviour in natura. OFT models has for a long time been criticized for sweeping under the carpet the key questions of the evolutionary dynamics and the maintenance of the optimal strategy in a population [9,10]. The distribution of available options is susceptible to change rapidly due to modifications of the environmental conditions or, even more simply, the presence of competitors which continuously remove the best options from the pool of available options [11]. The key point here is that the constant monitoring of available options implies cognitive (neural tissue is one of the most metabolically expensive tissues) and ecological costs: assessment and adjustment to the environmental conditions requires time, energy, and occasional mistakes (cost of naiveté, [12]). While rarely considered in optimal analyses, these costs should severely constraint the evolution of the subtle decision rules. Under rapidly fluctuating conditions, it could be more profitable to maintain a sub-optimal strategy (but performing reasonably well on the long run) than paying the far from negligible costs implied by the pursuit of optimal strategies [13,14]. For instance, in the analysis presented in this preprint, it is striking how close the fitness gains of the plastic and the non-plastic forager are, particularly if one remembers that the last-mentioned cognitive and ecological costs have been neglected in these calculations. Yet, even if one can arguably question its descriptive value, such models are worth more than a cursory glance. They still have normative value insofar that they provide upper bounds for the response to modifications of the environmental conditions. Such insights are precious to design future experiments on the question. Being able to compare experimentally measured behaviours with the extremes of the null model (stubborn non-plastic forager) and the optimal strategy (only achievable by an omniscient daemon) informs about the cognitive bias or ecological costs experienced by real life foragers. I thus consider that this model, and more generally most OFT models, are still a valuable framework which deserves further examination.

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Reviews

Evaluation round #2

DOI or URL of the preprint: **10.1101/273557**
Version of the preprint: 2

Authors' reply, 18 September 2018

Thank you for the positive reviews and for the specific suggestions to make the article more readable. We have incorporated the remaining suggestions into the revised version.

Decision by Francois-Xavier Dechaume-Moncharmont, posted 18 September 2018

Minor revision

Dear Authors

Both referees were satisfied with the new version of your manuscript. I have also carefully read through it and I agree that most of the previous concerns were satisfactorily addressed. I think that this new version has greatly improved the paper's clarity, and I thank you for this work. I am ready to write a recommendation for this study. Yet, as PCI Ecology does not copy-edit the preprints, the editors strongly advise their recommenders to pay particular attention to typographical and other minor issues. I do indeed have some comments that you should address prior recommendation, if you agree. As these points are only minor modifications, I believe you should be able to send the final version of your manuscript very soon. During this final edition of your pre-print, please pay attention to any typo, to the writing, or to the homogeneity of the reference list (particularly regarding the format of the journals' name). While I acknowledge that the presentation of the dummy variable x (lines 107 and followings) has been greatly improved, I still find that the rationale and the interpretation of what is fundamentally a mathematical trick deserve greater care to improve its understanding by non-theoretician ecologists. Please explain in plain sentences how to interpret this variable which is central in the rest of the text and in Fig. 3.

Speaking about Fig. 3, it is the key figure because it summarizes most of the results. It is crucial that this figure is understood by the largest possible readership (regardless of their complete understanding of the first part of the proof). I still consider that the axis names are not clear enough to be appreciated alone. Please, provide at least in the legend a simpler interpretation (see for instance lines 192-193) of these somewhat complex notations, or you will lose most of your reader, contributing to widen the gap between theoreticians and non-theoreticians.

Lines 209-220 and Fig. 4. – While I find such results particularly interesting, I do not understand exactly how was carried out the numerical calculation. Please, could you provide more information about the methods, particularly as regards the "gradual" adjustments of the strategy?

Abstract – the notation $\rho_\INTRA\$ is not defined so far. I am convinced that such a notation can be removed from the abstract without loss for the reader: "... the initial pattern of patch-exploitation in a habitat, as characterized by the regression slope of patch yields...".

Fig 1 legend – The mathematical notation E^*_n is not defined so far, neither in the legend (the legend is not self-sufficient) nor in the main text when the figure is called for the first time (lines 24). The first complete definition is only to be found much later, lines 63.

Fig. 2 legend – same comment as in the abstract about the notation $\rho*INTRA\$. In addition, there is probably a mistake about the figure name in the middle of the legend: "...within the habitat $\rho*\INTRA\$. In (a) they have greater absolute yield...". One should read "in (b)", I suspect. Please carefully check also the other figure names in the rest of the text.

Fig. 3 – The intriguing circled points are not defined in the legend. One has to wait Fig. 4 for an explanation. Please be sure that the figures their legend are self-sufficient.

Line 156. The terms "ballistic" is somewhat unusual. Do you really need such a non-trivial term here? More generally, the term "systematic" is not used any more in the rest of the main text. Instead you are using the terms "plastic vs. non-plastic forager". Please use a consistent terminology to avoid confusion.

I am really concerned by the fact that most theoretical papers must be understood by non-theoretician ecologists if we want to really push our field forward. I thus recommend to avoid informal mathematical shorthand such as l.h.s (for the left-hand side) or r.h.s. (lines 127, 130 and 229). There is no space limit for preprints.

Reviewed by **Andrew Higginson**, 03 September 2018

The authors have responded thoroughly and effectively to all the reviewer comments and I have nothing further to add.

Reviewed by **Frederick Adler**, 30 August 2018

The authors have done a nice job of responding the comments, and I like the improved clarity of the new figures and the broader framing of the issues, and am I happy to recommend this paper.

Evaluation round #1

DOI or URL of the preprint: **10.1101/273557**
Version of the preprint: 1

Authors' reply, 31 July 2018

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Decision by **Francois-Xavier Dechaume-Moncharmont**, posted 31 July 2018

Revision needed

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?

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

Reviewed by Andrew Higginson, 11 May 2018

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Reviewed by anonymous reviewer 1, 28 March 2018

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