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RECOMMENDATION

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Andrew Higginson and Frederick Adler

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A recommendation of

Calcagno V, Hamelin F, Mailleret L, and Grognaud F. How optimal foragers should respond to habitat changes? On the consequences of habitat conversion. *bioRxiv* 273557 (2018), ver. 4 peer-reviewed and recommended PCI Ecology. DOI: 10.1101/273557

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 [7]. 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 [12]. 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 [10].

This preprint [3] is in line with the long-established literature on OFT. It follows two theoretical articles [2, 4] 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

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paradox which occurs when the aggregation of subgroups modifies the apparent pattern at the scale of the entire population [8, 9]. 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 these 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 carefully 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 have 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 [1, 13]. 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 [5]. 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, [14]). While rarely considered in optimal analyses, these costs should severely constrain 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 [6, 11]. 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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Appendix

Reviews by Andrew Higginson and Frederick Adler, DOI: 10.24072/pci.ecology.100005