

Response letter round 2

Dear Authors,

Thanks for your revisions and for your detailed responses to the comments. The changes have addressed almost all of the prior queries, and I would like to recommend this article for PCI, and I still have a request for changes to the section on Disturbance Scenarios. I apologize for the delay, it was partly due to needing to take the time to work out the questions I had about your formulation and response to the prior reviews.

My main question is the similar to one I posed in the original review, but I think I can express it more clearly now. A foraging animal could keep track of total time foraging in a patch, and have a leaving rule that is to leave at a constant time within the patch. This is the formulation that you have adopted. You point out that the average gains for spending t time units in a patch depend on the actual time spent foraging (which is lower than time in the patch) and the variance in time spent foraging (because the gain curve has negative second derivative). There may also be a direct cost of disturbance, which you include in eq 2.

An alternative assumption about forager behavior is that they may be able to track how much time they spend actually foraging in the patch. In other words, they could track t_f , time foraging in the patch, t_v , time being vigilant in the patch, and then $t=t_f+t_v$ is total time in the patch. They could have a rule to leave at a specific t_f . This gives a average return function of

$$f[t_f] / (T + t)$$

Taking the derivative with respect to t_f and solving for it being 0 gives

$$f'[t_f] = (\beta + \gamma) f[t_f] / (T \gamma + t_f (\beta + \gamma))$$

I believe that this solution will have higher average fitness than the rule of leaving after a fixed total amount of time in the patch since it allows the animal to use more information. I believe that it would be valuable to relate the “fixed total time in patch” rule to a “fixed foraging time in patch” rule, even if only to say these are alternative assumptions about how forager decisions could be made.

Thank you for your careful reading. You are correct that, in the Disturbance case, we may just as well formulate the problem in terms of the foraging time (t_f) rather than actual time t . This is a possibility we've contemplated. However, proceeding with t_f does not yield a MVT-like equation: the equation you have derived is not of a MVT form. We might transform it into one by rescaling the travel time appropriately, but this can only work in the homogenous case (all patches identical), not in general. In contrast, our formulation in terms of t naturally yields a MVT-like equation, and since the purpose of the article is precisely to show how risk can be incorporated into a MVT framework, we have retained the latter.

In terms of fitness and predictions, the two ways to proceed (i.e. leaving at some effective foraging time t_f^* versus leaving at some residence time t^*) are essentially equivalent, at least in the situations we consider. We cannot expand on this here, but it can be shown that the two strategies become equivalent as β and γ get large, and this is the situation we are interested in (i.e. short and frequent interruptions). As a matter of fact, the mere statement that the residence time t equals $t_f * (\beta + \gamma) / \gamma$ already requires this assumption, so that both formulations hold only under this limit, under which they are effectively undistinguishable. A

rigorous mathematical qualification would be out of scope, but numerics are revealing enough:

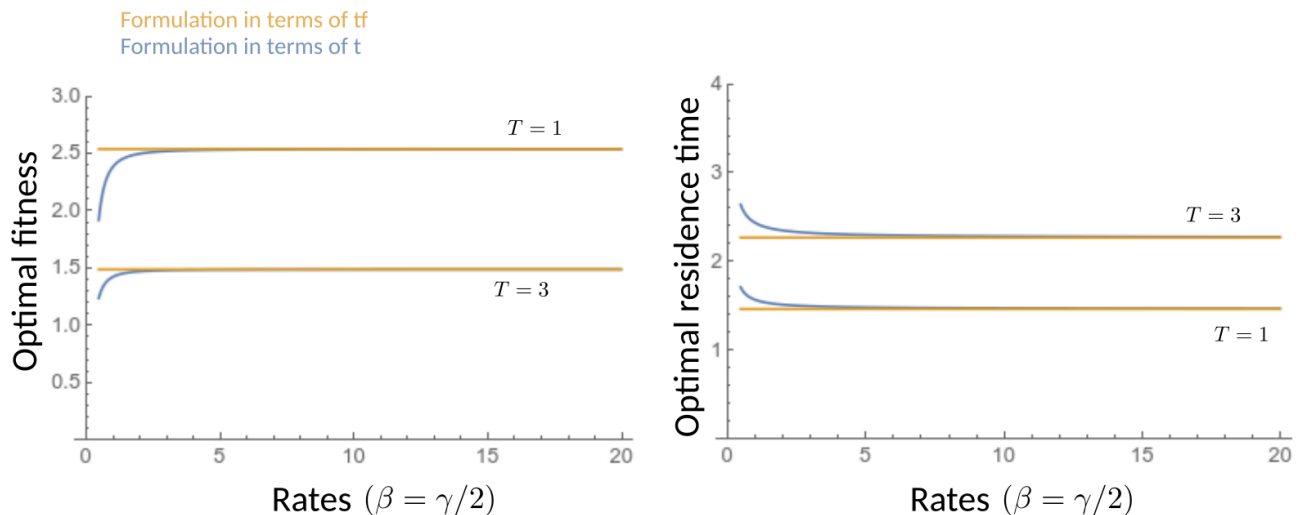


Figure: Comparison of results obtained by maximizing (numerically) the fitness proxy expressed in terms of either effective foraging time (orange) or residence time (blue). The interruption rate β was increased from zero, and the recovery rate γ was set at 2β , so that the individual was actively foraging on average 66% of the time. Two travel times values were used ($T=1$ and 3), with the same gain function as in the article.

It can be seen that as soon as rates are greater than about 2-3 the two approaches yield identical fitness and optimal residence times (for reference, in the article we consider values in the range 0-100). Below 2-3, both formulations break down anyway (as the relationship between t_f and t becomes more complex). Furthermore in such situations (rare/long interruptions) the particular gain functions become so irregular (step-like) that the type of optimal strategy changes: it would imply leaving with no delay when the first interruption (or maybe the second) occurs. This quickly converges to the situation we analyze in the second scenario (Escape scenarios): an individual leaves as soon as an interruption occurs.

We have made some changes in the article to better address the significance of t_f and the possibility of a leaving-rule based on it:

- We now state more clearly the assumptions made in our derivation, in particular the fact that interruptions are assumed to be short and frequent in Disturbance scenarios (lines 153-155; see also our response to your next point regarding equation (2)).
- We now indicate as a possible leaving rule the monitoring of effective foraging time (lines 382-384). We explain that since resource density is a direct function of t_f , such a leaving rule has exactly the same implications as the GUD-rule. Therefore, results presented in Figure 5 comparing the consequences of a time-based versus a GUD-based leaving rules also apply to the t_f based rule you suggested.

We believe that with these clarifications, no ambiguity remains.

Fundamentally, I think it is important to note what assumptions go into the version presented in the paper. The presentation around eq 2 does not explain verbally how the equation was derived, although you do a great job of explaining what the terms in eq 2 represent. Before presenting eq 2 you should explain that the assumption is that the animal can only track total time in the patch. As you explained in your response letter, it cannot directly assess the current patch quality.

We agree that the derivation of eq (2) was elliptic in the main text. We have provided more explanations regarding the method and the assumptions made (lines 149-151). We in particular stress that this scenario considers rather frequent and short (relative to a patch visit) interruptions (lines 153-155). If interruptions get sufficiently rare and long lasting, then pretty quickly an individual should leave as soon as it is interrupted for the first time, and the situation becomes the scenario considered in the next Section (“Escape scenarios”). We have added a sentence to underline this point (line 179).

by **Stephen Proulx**, 19 Apr 2024 15:56

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