The importance of travel time in foraging theory models

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21 August 2013

Additional analyses and discussion to accompany:

> Wikenheiser AM, Stephens DW, Redish AD (2013) Subjective costs drive overly patient foraging strategies in rats on an intertemporal foraging task. *Proc. Natl. Acad. Sci. U. S. A.* 110(20): 8308-8313.

After publication of our article examining foraging strategies in rats (1), we were made aware of an additional model that could potentially explain some aspects of the observed behavior. The foraging model developed in the paper (eq. 1) does not include a travel time term, and thus computes the food intake rate only over the delay periods at feeder sites. This formulation is consistent with the finding that animals in intertemporal choice scenarios often disregard the intertrial intervals between decisions (2–5). However, a model incorporating travel time into the rate calculation could yield different results.

Accordingly, we reanalyzed our data using a rate model with travel time included:

$$R = \frac{\sum_{i=1}^{3} p_{wait_i}}{T + \sum_{i=1}^{3} p_{wait_i} delay_i}$$

When T (travel time) was set to 6s, as measured from rats' behavior on the task (1), subjects achieved a mean food intake rate ~85% of the maximal rate, compared to only ~47% as computed using the model lacking travel time. Behaviorally, this suggests strategies fell closer to rate-maximization under the model including travel time. However, when we fit the A parameter using eq. 2 (1) with the 6s travel time factored in, the best fitting A values remained non-zero and significantly correlated with opportunity cost (P = 5.02 x 10-9, R^2 = 0.22), as reported in the paper.

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It is also possible that rats were optimizing intake rate with respect to a subjective variable related to travel time, perhaps influenced by factors such as the effort cost of running, whether time spent running is treated the same as stationary time spent waiting, and accuracy for time interval perception. Such an effect could be captured by a rate model that includes a cost factor *c* multiplied by *T*. However, to accommodate the shift in willingness to wait subjects showed across session types (1), *c* would need to vary with opportunity cost, much like the *A* parameter we proposed (1). Thus, whether placed in the numerator or denominator of the rate equation, casting behavior on our task as rate-maximization requires invoking a subjective factor akin to the *A* parameter detailed in the paper (1).

Acknowledgements

The authors thank Nathaniel Daw for helpful comments.

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