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Published in:
Proceedings of the National Academy of Sciences of the United States of America

Link to article, DOI:
10.1073/pnas.2025720118

Publication date:
2021

Document Version
Publisher's PDF, also known as Version of record

REPLY TO LETTEN AND YAMAMICHI:
A rescue at the cost of falsifiability

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Letten and Yamamichi (1) make valuable comments about our recent paper (2). They point out that the gleaner–exploiter trade-off commonly refers to population growth rates and not prey consumption (the focus of our study). We agree and should have made our reasoning clearer. We assume that food consumption and population growth rates are positively associated; therefore, a positive association between maximum ingestion rate (I_{max}) and maximum clearance rate (C_{max}) reflects a positive association in population growth rates at high and low food concentrations. Letten and Yamamichi argue that we may have overlooked a trade-off in population growth rates through two possible mechanisms.

The first mechanism is systematic variation in conversion efficiency. We concede this point, having included the same argument in the paper as a caveat; we also included data that lends support to our assumption.

The second mechanism is a negative association between mortality rate and I_{max} and/or C_{max}. Two aspects to this are worth distinguishing between:

1) The authors (1) focus on predation-induced mortality, the major source of mortality in nature. They argue that the foraging–predation risk trade-off that we implicate is a gleaner–exploiter trade-off: More foraging leads to an increase in predation-induced mortality, which increases R* (lower is better), I_{max}, and C_{max} (higher is better). We think this argument is misguided for the following reasons:

i) *R** is best understood as the minimum required resource concentration in the absence of predation. This is consistent with prior theoretical usage (3, 4) and most empirical studies characterizing *R** (5, 6). If we were to include predation losses, *R** would no longer be a property of a population but a joint function of every population and its predation environment. Consequently, evaluating the gleaner–exploiter trade-off would require arbitrary choices of predation pressure for each species. This framing therefore makes the putative trade-off highly context dependent at best and unfalsifiable at worst.

ii) Moreover, we already have a term for a function characterizing the minimum resource requirement across a gradient of predation pressure: It is a form of zero net growth isocline, or ZNGI (3, 4). Such a ZNGI intercepts the resource axis at the *R** as we define it above (3, 4).

iii) If the trade-off between foraging and predation risk is by definition a gleaner–opportunist trade-off, as Letten and Yamamichi (1) argue, the latter concept has lost the specificity that makes it useful. It instead becomes a stand-in for a class of different trade-off mechanisms. We agree that a gleaner–opportunist trade-off may emerge from the more fundamental foraging–risk trade-off under certain conditions but prefer to retain separate terminology for the distinct mechanisms for clarity.

2) Background mortality captures losses due to factors other than predation; the simplest natural analog is death due to old age. If background mortality rates are strongly positively associated with I_{max} or C_{max}, then there could indeed be a gleaner–exploiter trade-off that we overlooked. This is a useful caveat to our results, and we thank the authors (1) for pointing it out. We believe such a relationship is unlikely, but this cannot be ruled out due to the lack of data.

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Author contributions: T.K. and M.K.T. wrote the paper.

The authors declare no competing interest.

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Published January 25, 2021.

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