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INTRODUCTION TO THE INVITED REPLY

What Is, and What Good Is, Fitness? Reflections on Takacs and Bourrat

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1. Recently Takacs and Bourrat (2022) published a critique of several philosophers' uncritical endorsement of a geometric mean definition of fitness that is supposed to better explain evolution in changing environments compared to fitness defined using an arithmetic mean. One locus of criticism was the relative inability of geometric mean fitness to capture natural selection in scenarios with overlapping generations. Instead they argued that the instantaneous growth rate provided a better measure of fitness. In response, Autzen and Okasha (2022) agreed with the critique of geometric mean fitness as *the* definition of fitness. However, taking into account both deterministic and stochastic selection scenarios, they concluded that the long-run growth rate is a better measure of fitness and is, in fact, analogous to geometric mean fitness. They call for pluralism about measures of fitness.

The piece that follows is Takacs and Bourrat's response to Autzen and Okasha's criticism. Autzen and Okasha have decided not to comment any further and the purpose of this introductory note is to take stock of what has been learnt and perhaps close this round of the seemingly unending philosophical debates about the concept of fitness in evolutionary biology. The point that Takacs and Bourrat emphasize is that Autzen and Okasha are concerned with stochastic scenarios while their focus is on deterministic ones. However, as footnote 2 of their response admits, their original language had been misleading and, so, Autzen and Okasha cannot be blamed for interpreting them otherwise.

2. The first point that should be emphasized is that the exchange so far shows that there were more points of agreement than disagreement between the two sides. There was agreement that philosophers were wrong to endorse geometric mean fitness as *the* definition of fitness. In retrospect, the apparent philosophical agreement on this point goes to show how shallow were the original philosophical discussions of fitness in the 1980s and later. Moreover, the apparent technical differences between the two sides are also easily resolved once three distinctions are clearly articulated: that between discrete and continuous time dynamical models of population change, that between nonoverlapping and overlapping generation models, and that between finite and infinite population models (that is to say, stochastic and deterministic models). In their very useful Fig. 1 Takacs and Bourrat illustrate how, once these distinctions are kept to the forefront, the conceptual apparatus underlying the three papers can be explicated.

Both sides are also convinced that nonoverlapping generation scenarios are biologically rare. But this seems to be a misplaced assessment. Autzen and Okasha (2022, p. 37) write, "it is true that only a few species (such as 13-year periodical cicadas) correspond exactly to the assumptions of a discrete-time growth model with non-overlapping generations." But this claim is odd; it ignores the fact that every annual plant (or, for that matter, biennial plant) has nonoverlapping generations. Even if we take into account the existence of seed banks that can maintain viable seeds for multiple generations without germination, the scenario still maintains nonoverlapping generations. That is why even complex cases of plant evolution (for instance, the emergence of self-incompatibility alleles—see, e.g., Levin et al. 2009) are modeled in this fashion. Many insects such as solitary bees also have nonoverlapping generations. I suspect that this is a case of being misled by intuitions derived from the biology of large animals, a severe and common problem in the philosophy of biology.

3. Autzen and Okasha explicitly call for pluralism about measures of fitness. Takacs and Bourrat are less explicit, perhaps because they focus on the work of philosophers of biology rather than that of biologists. This call for pluralism

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is one that philosophers of biology should heed. What is puzzling, and perhaps worth historical exploration, is why philosophers ever assumed that there is a single concept of fitness. The founders of modern evolutionary theory—Haldane, Fisher, and Wright—made no such claim even though Wright is the source of the most common representation of fitness in models of selection (Sarkar 2007b). While Fisher (1930) used a multiplicity of fitness measures, including several of the ones invoked in this exchange (e.g., the Malthusian parameter), Haldane (1924) preferred the intensity of selection in place of fitness but was eclectic in his use of fitness measures (Haldane 1932; Sarkar 2017). Crow and Kimura's (1970) pathbreaking textbook endorsed this pluralism even though it mostly used Wright's popular measure.

In fact this pluralism raised the question of how important the concept of fitness is for evolutionary biology even if it is accepted that natural selection is the major factor of evolution (which I believe to be open to question; Sarkar 2007a). All of the disputants agree that how evolution should be theorized (or, what is mostly the same thing, modeled) depends on the context: the scenario and the question being asked. Perhaps invoking an instantaneous or long-run growth rate could be regarded as alternative concepts to fitness rather than measures of fitness. Such a choice may finally put to rest the philosophical disputes about the interpretation of fitness that, as far as I can tell, have had no operational impact on the practice of evolutionary biology.

4. As Autzen and Okasha also note, pluralism about concepts of fitness also raises the question as to what constraints should be imposed on any measure to count as embodying a concept of fitness. Though they do not use this terminology, they are asking for adequacy conditions for fitness conditions. They ask for further philosophical reflection on this problem and that may well be more important than their critique of Takacs and Bourrat. They also note that there is some consensus among biologists that the most relevant criterion is whether fitness increase can be used to determine whether one type can replace another one. (The motivation for this adequacy condition lies in Maynard Smith's game-theoretic analysis of evolution using so-called evolutionarily stable strategies (ESS).)

If we accept this as the most relevant criterion, then fitness considerations may well turn out to be questionable when it comes to radical macroevolutionary change, when there is a major transition that results in novelty rather than within-type changes. Can the ideas of ESS be generalized to include situations such as new body plans emerging without old ones being replaced? Or, perhaps, formal fitness-based arguments can never get us beyond microevolution.

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