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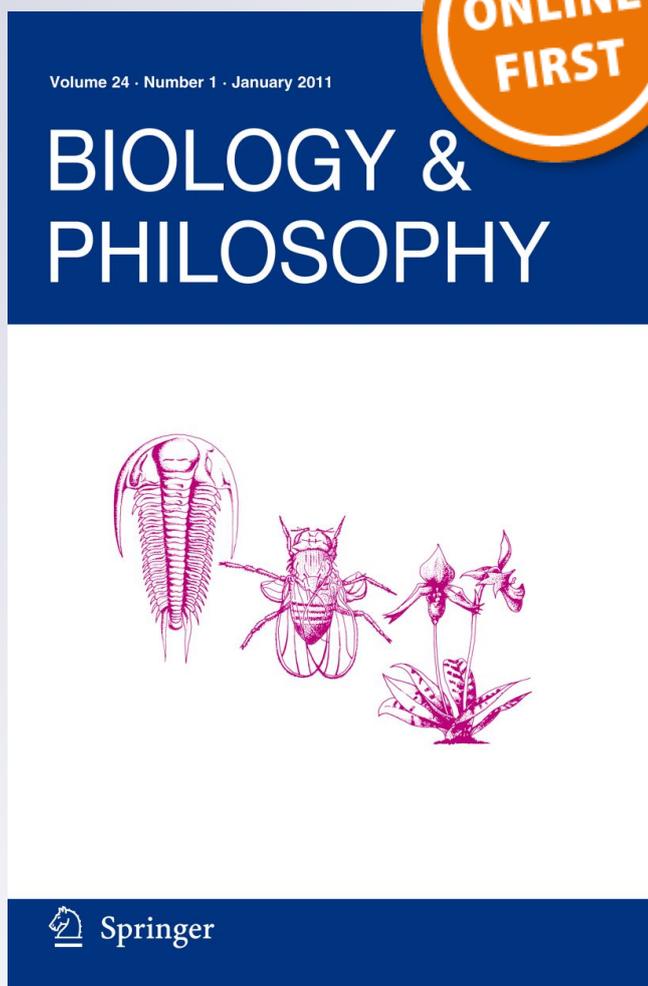
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Biology & Philosophy

ISSN 0169-3867

Biol Philos

DOI 10.1007/s10539-012-9333-3



 Springer

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Received: 14 November 2011 / Accepted: 7 July 2012
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Abstract In a recent paper, Potochnik (Biol Philos 24(2):183–197, 2009) analyses some uses of optimality modelling in light of the anti-adaptationism criticism. She distinguishes two broad classes of such uses (weak and strong) on the basis of assumptions held by biologists about the role and the importance of natural selection. This is an interesting proposal that could help in the epistemological characterisation of some biological practices. However, Potochnik's distinction also rests on the assumption that all optimality modelling represent the selection dynamic involved in the system of phenomena being considered. Since this assumption does not hold for models belonging to optimal foraging theory (OFT)—one of behavioural ecology's important modelling traditions—Potochnik's proposal has to be critically reappraised. In this paper, we briefly discuss what is optimality modelling and what it means for a model to represent a dynamic of selection or of evolution. Then, we demonstrate that OFT modelling is unable to represent either past or contemporary selection dynamics. In order to make this point, we carefully delineate the theory's rationale. This allows us to identify and analyse the assumptions on which the theory is built, and to circumscribe precisely the role that natural selection plays in it. Next, we show that the distinction of weak and strong uses of optimality modelling is seriously weakened when OFT modelling is taken into account. More

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precisely, the distinction is either irrelevant (if the assumption that selection dynamics are represented in all optimality modelling is held) or of a modest utility (if the assumption is dropped). However, we suggest that Potochnik's original proposal could be saved, and that it even constitutes a tool to appraise the marks left in the literature by the evolution of optimality modelling practices in the last four decades, provided that it is made into a tripartite distinction.

Keywords Adaptationism · Optimal foraging theory · Optimality · Fitness · Animal behaviour · Behavioural ecology

Introduction

The topic of adaptationism has attracted much attention in the last two decades. With the recent celebration of the 30th anniversary of Gould and Lewontin's *Spandrels* (1979) came an interesting opportunity to assess the conceptual progresses made since. As it now seems consensual that there is no single definition of adaptationism, it is possible to characterise it in different ways. If we follow Lewens' (2009) analysis, adaptationism can be used as an epithet to refer to four distinct sets of statements: 1° Statements on the power, the directness and the historical manifestations of natural selection in evolution (empirical adaptationism); 2° those about evolutionary biology's methods (methodological adaptationism); 3° those about people's interest for adaptations (disciplinary adaptationism); and those about our confidence toward descriptions of adaptations and adaptive traits (epistemological adaptationism). While these characterisations took shape (see also Godfrey-Smith 1999, 2001), the notion of adaptation was being critically appraised and recast according to particular scientific problems such as cumulative selection (Nanay 2005), simplistic adaptive explanations (Barker 2008) or its relations to natural selection and constraints (Shanahan 2008). If we bear in mind these numerous conceptual refinements and specifications, it is surprising that some philosophers of biology still consider the subject of optimality modelling as a single monolithic practice, and raise the possibility that the whole package could be branded "adaptationist". This was obvious in the challenge raised by Orzack and Sober (1994a),¹ although its relevance was later contested by Abrams (2001). More importantly, it is also a significant feature of Potochnik's (2009) analysis on the subject.

Summarily, Potochnik distinguishes two sorts of uses of optimality models. These two sorts are inferred from what scientists think their optimality models

¹ Through the 'Adaptationism Project', Orzack and Sober propose a method for testing the thesis of empirical adaptationism. Summarily, it requires a three part test. Firstly, the optimality model's predictions must be compared to observations of the natural system of interest and assessed quantitatively. Secondly, whether or not the within-population heterogeneity in phenotype is consistent with the variation predicted by the model must also be assessed. Lastly, it is necessary to conduct an ensemble test on the highest possible number of studies using an optimality model. By quantifying how many independent studies succeed in completing the two first parts of the test (that is, whether 1° there is a quantitative fit between modelling and observations, and 2° the observed inter-individual heterogeneity is accounted for in the model), it could be possible to prove or disprove the thesis of adaptationism (Orzack and Sober 1994b).

represent. According to this proposition, the ‘strong use’ of optimality modelling describes those uses in which natural selection is represented as the only important factor in the evolution of the considered phenomenon, whereas the ‘weak use’ describes the uses in which natural selection is more modestly construed as one of the factors responsible for the evolutionary dynamics in which a trait is imbedded. Said otherwise, the two sorts of uses can be distinguished by the role scientists impart to natural selection in their formal depiction of the evolution of a given phenomenon. This distinction is very interesting since it allows the drawing of a rather clear line between claims that commit to adaptationism and those that do not. Indeed, according to Potochnik’s analysis, the weak use is credited for leaving enough room to study other factors involved in a trait’s evolution, namely constraints and genetic drift, and thus of being decoupled from the question of empirical adaptationism (*sensu* Godfrey-Smith 1999 or Lewens 2009). In principle at least, the distinction could be a useful tool to detect and appraise the epistemological shift that Gould and Lewontin anti-adaptationist criticism (1979) might have initiated within the biological literature.

However, Potochnik’s characterisation of optimality modelling has a flaw. It rests on the assumption that optimality models make up a rather homogenous class that shares different properties. Although this could be true for some properties, it is not the case for the one that sets the stage for the distinction between weak and strong uses. Indeed, throughout her analysis, Potochnik insists on the fact that optimality models represent the selection dynamics involved in producing the evolutionary outcome of interest. In other words, she claims that models belonging to the optimality kind depict or represent the involvement of some of the factors (mostly natural selection, according to the author) involved in the evolution of a trait. This assumption oversimplifies the practice of optimality modelling. Indeed, and although Potochnik’s characterisation of the weak use describes something relevant to the contemporary biological practice, it dramatically fails to account for one classical and very important use of optimality modelling in behavioural ecology. Indeed, the overall success of the optimality approach is largely due to its prominent role in the advancement of behavioural ecology, along with the development of optimal foraging theory (Stephens and Krebs 1986; Cézilly 2008).

In this paper, we have two main goals. Firstly, we would like to argue that the scope of Potochnik’s proposition has to be carefully assessed. Indeed, the distinction of weak and strong uses does not hold for all forms of optimality modelling. Secondly, and in order to substantiate our call for caution, we would like to scrutinise a form of optimality modelling that compromises the ‘weak and strong uses distinction’ such as it is grounded by Potochnik on the model’s capability to represent selection dynamics. Thus, we intend to demonstrate that one of optimality modelling little gems, namely optimal foraging theory, does not allow to make any claim on either the pre-eminence of natural selection in the past evolution of traits, or the current shaping of traits by natural selection. In short, optimal foraging theory (OFT) is unable to represent a dynamic of selection. This, as a matter of fact, is enough to guarantee OFT’s imperviousness to the main anti-adaptationism criticisms. In the field of behavioural ecology, OFT is simply used as a tool to investigate the current factors (parameters and variables that summarise either an

organism or an environmental feature) that are causally linked to the behaviour of individuals.

Our paper will be subdivided into six sections. In the first one, we draw a general picture of what is usually understood as the practice of optimality modelling. This schematic portrait will then be used (section “[Modelling and the representation of a dynamic](#)”) to analyse the assumption on which Potochnik’s distinction rests, that is the representation of selection dynamics by models. The next two sections will introduce and analyse the use of optimality that seems to be compromising the distinction’s very foundations. Indeed, in section “[Optimal foraging theory](#)” we will introduce optimal foraging theory as a sort of modelling that is unable to represent any kind of evolutionary dynamics. In section “[Optimal foraging and natural selection](#)”, we will lengthily analyse the assumptions on which OFT rests. This, in turn, will allow us to demonstrate why the representation of selection dynamics falls outside of OFT’s representational capabilities. In section “[The weak and strong uses of optimality modelling](#)”, we will assess the relevance of Potochnik’s distinction in light of the shortcomings revealed by our analysis of OFT. In order to do that, we subdivide Potochnik’s proposal into two propositions. Finally, in section “[Neither strong nor weak, but heuristic](#)”, we argue that the distinction of weak and strong uses needs to be supplemented with a third sort of optimality modelling uses, the heuristic uses. This, by providing Potochnik’s original suggestion with a more comprehensive framework, could allow for subtler historical and philosophical accounts of the optimality modelling practice. So we hope.

Optimality, a multi-use tool

Optimality modelling has to be construed as a generic appellation for a cluster of different modelling practices. Although these practices have been refined individually, they all have been thoroughly influenced by developments in biology, and more especially in ecology. This is obvious in the way optimal foraging theory got established (Emlen 1966; MacArthur and Pianka 1966) and gathered momentum. But it is certainly the contribution of evolutionary game theory, ever since Maynard Smith and Price’s (1973; Maynard Smith 1982) founding work, that has brought optimality modelling its current pre-eminent status by giving it a whole new dimension. Indeed, this approach of optimality has plainly demonstrated that evolution is not simply a matter of organisms being optimal in some of their features. Individual traits (tactics or strategies in evolutionary game theory’s vocabulary) evolve as parts of wholes, and their evolution is shaped by a broad diversity of constraints (heredity, morphology, development) and “processes” (natural selection, mutations, drift, phylogenetic inertia). Thus, it comes as no surprise that some strategies demonstrated to be stable within the evolutionary game theory’s framework—that is, strategies that are either evolutionary stable or unbeatable²—are not in fact those that truly and absolutely maximise the organism’s fitness. What

² An evolutionary stable strategy (ESS) is a strategy that cannot be invaded by a mutant strategy that may arise (Maynard Smith and Price 1973), whereas an unbeatable strategy is one that cannot be outmatched by any alternative strategy whatever its starting frequency (Hamilton 1996). Although some scientist tend to equate the two notions (see, for instance, Nowak and Sigmund 2004; McGill and Brown 2007),

is evolutionary stable is not necessarily what includes ‘the best possible design for the whole’, as it has been held in the past (Gould and Lewontin 1979).

This being said, identifying a trait that does not seem to contribute optimally to the organism’s fitness raises two questions of interest for our argument: what is an optimal trait and how do biologists define a trait’s optimality. Firstly, what does it mean for a trait to be optimal for a particular class of organisms? Simply put, it means the feature of interest maximises (or minimises) some quantity in a given context. More precisely, it means the feature is such that it *could* make the highest contribution to (or take the lowest toll on) the organism’s inclusive fitness, given its current developmental, physiological and environmental characteristics (i.e. constraints that impinge on the trait). We use the conditional because the confirmation of a claim about a trait’s contribution to fitness requires 1° that this contribution is appraised against that of at least one of its variants (either naturally occurring or theoretical), and 2° that this contribution to fitness is actually measured for the organism’s class of interest, some way or the other. Therefore, claiming a trait is optimal does not entail that the feature of interest has been selected for itself, or that it is actually possible to demonstrate that some of its characteristics have been influenced by some selection regime or another. This will become obvious in section “[Optimal foraging and natural selection](#)”.

Secondly, how is a trait’s optimal state defined in optimality modelling? Said otherwise, how is it that biologists are able to hypothesise on and approximate the value of a feature’s optimal state, especially if that value is seldom if ever actualised in nature? As a preliminary answer to both phrasing of the question, we can underline the fact that defining the optimal state a character could take heavily relies on the appraisal of correlations and causal relations at play in the biological system. It is some of a trait’s characteristics, and relations to other features (assessed either in the wild or in the lab), that allow the hypothesising of an optimal state, and the design of an optimality model. Hence, the minimal requirement to hypothesise the optimal state of any phenotypic feature—and this is true whatever the way a character is defined and individuated—is, at least, a superficial knowledge of the organism of interest (Pyke et al. 1977). It is fortunate that this knowledge cannot be dispensed with because precise empirical work is also required in order to appreciate the way in which and to what extent the actual organism’s trait departs from both its formal representation and the hypothesised optimal state. Said otherwise, the trait’s actual determinations and its constitutive mechanisms are of critical importance both to model the hypothetical optimal state, and to appreciate the empirical adequacy of the description. Of course, a qualitative or quantitative fit (or lack thereof) between the formal description and empirical data can be quite inspiring. But it is important to underline that a fit’s main role is to provide an assessment of the accuracy with which the mathematical formalism accounts for the trait’s design. In itself, optimality is an appraising tool, not a hypothesis submitted to empirical verification (Maynard Smith 1978; Stephens and Krebs 1986). In other words, what is being assessed when model and data are

Footnote 2 continued

Hamilton’s definition is more stringent (Sigmund 2001) and could prove useful in evolutionary games in which migration has to be taken into account.

compared is not whether some trait is optimal, it is whether the model's parameters and variables succeed in capturing some of the trait's features, some of the relations it is involved in. Seen in this light, it is probably becoming obvious that optimality modelling can be used to investigate something other than evolutionary dynamics, contrary to what is suggested by Potochnik's paper. Before we undertake to show how this type of modelling is carried on, and before we analyse the sets of assumptions it is based on, it is necessary to examine what it means for an optimality model to represent a dynamic of selection.

Modelling and the representation of a dynamic

It is indeed a truism to underline that not all mathematical models are designed to provide dynamical representations of phenomena. Some are simply used to statistically infer relationships among the various components of a system, such as in attempts to establish metabolic networks or to map quantitative traits onto a genome (Daigle et al. 2010). If we strictly focus on those models that represent dynamics of evolution, it is obvious that they share two essential features. Firstly, they account for the correlated changes in some quantities over a time interval. This is true whether we consider the frameworks of sexual selection models (Kokko et al. 2006), of logistic equation models (such as those based on the Lotka–Volterra equations), of evolutionary game theory models, of evolutionary game theory models embedded in logistic equation models (Vincent and Brown 2005), and so on. The quantities modelled to change can be of various kinds, according to the framework used (trait values, densities of population's members, frequencies of phenotypes, etc.), but the model's formalism has to be such that it accounts for a time interval when solved.

Although it can be dispensed with in the modelling of some other phenomena (where it is replaced by some condition of the system or by spatial coordinates), the time interval is a feature of absolute necessity for the representation of a dynamic of selection. Indeed, it is the sole 'component' along which the effects of selection or evolution can be construed. Borrowing Whewell (1840, Chap. 6, pp. 184–237) classical depiction of dynamics, time is the condition through which we conceive the motion (the correlated change in some quantities), and the forces that produce that motion (the so-called 'forces' of evolution) of evolution by natural selection. Expressed very succinctly, there can be no representation of evolutionary dynamics without the integration over time in the modelling.

Secondly, in order to represent a dynamic of selection—and not just any population dynamics such as those involving populations of prey and predators in the simplest use of the Lotka–Volterra equations—the model has to depict selection one way or the other. The way selection is introduced into a dynamic is directly linked to the framework the dynamics is construed in. For instance, in Lotka–Volterra model of competition, selection is brought in through the classical logistic equations' parameter r (rate of increase per individual), whereas it is introduced as a selection coefficient (s) or a selection gradient (β) in sexual selection models. It is not the place here to review, define and appraise the various parameters in use for the representation of selection dynamics in models. An interesting, if somewhat uneven, review of this can be found in Endler's *Natural Selection in the Wild* (1986, chap. 1).

Now that we have provided an outlook on both the general characteristics of optimality modelling and on what is required for mathematical modelling to represent dynamics of either selection or evolution, we can outline the features that should be found in optimality models able to represent such dynamics. To begin with, we have seen that optimality modelling describes how a focus trait relates both to some other 'traits' (developmental, physiological or environmental characteristics) and to the organism's inclusive fitness. This double correlation is the basis to formally describe the trade-off according to which the focus trait can be optimal. If we take for granted that natural selection is already depicted in all optimality modelling (we will see to what extent this is true of OFT in the next two sections), then what is needed for such a form of modelling to represent selection dynamics is that it includes 'time' as the component through which the dynamics unfold. As stated earlier, a time interval (or the integration over time, to be more technical) is needed in order to represent the changes that go with natural selection and evolution. The representation of these changes (the representation of a dynamic in Potochnik's terms), be they empirically observed or formally described, cannot be done independently of the depiction of a time interval. Now, it is our contention that although all optimality modelling represent a dynamic of some kind, not all of them represent a dynamic of selection or of evolution. This will have some consequences on Potochnik's distinction of strong and weak uses of optimality modelling. In the following sections, we proceed to describe the internal workings of a form of modelling, optimal foraging theory, in which the changing quantity's dynamic is not framed by using time.

Optimal foraging theory

Indeed, optimal foraging theory is used as a tool to investigate the current factors (parameters and variables that summarise either an organism or an environmental feature) that are causally linked to the behaviour of individuals. In order to understand this, it is important to analyse OFT's working and the assumptions it involves. To make things easier, investigations built within this framework follow a fairly straightforward five-step path. 1° From observations of an organism's behavioural repertoire, biologists delineate a decision (a trait) related to foraging and proceed 2° to identify what factors (both environmental and physiological) preside over the options open to decision. For instance, imagine a population of Great tit (*Parus major*) inhabiting a stable environment and feeding on two types of evenly distributed prey. The trait studied would be the proportion of each prey types that is consumed, and the factors taken into account would be such things as the nutrients and energy requirements of the bird, the nutrients and energy content of each prey types, the handling time they require, their availability, and so on. However, 3° optimality modelling truly begins with the definition of the variable to be optimised. It is only once it has been specified that it becomes possible 4° to formalise how the factors of interest relate to it. In the above example, the variable to be used would be a summary of both the nutrients and energy intakes per time unit. After the model is built, or after the formal representation is drawn, biologists then 5° proceed to test it empirically. This allows the assessment of whether the

factors used in the model are relevant for the decision under scrutiny, that is, whether these factors are causally linked to the delineated behaviour. More precisely, a close match between some of the model's predictions and empirical results leads to two complementary conclusions: the organism is indeed acting optimally in the environmental context it is depicted in; and the model is working well within a particular range of parameters. However, it is the discrepancies between some of the model's predictions and data that seem to be the most fruitful for the understanding of behaviour. Indeed, such failures prove important because they require scientists to refine their model, if not their initial hypotheses: some important parameters might have been neglected, or the decision being investigated may be subordinated to other aspects of foraging, thus being constrained in unforeseen manners. But long before the foraging hypothesis is empirically tested, some prior knowledge of the organism of interest is a prerequisite to optimal foraging theory. This knowledge is critical for the construction of the optimality scenario, being introduced through the specific assumptions it involves.

Optimality models used in OFT are necessarily framed according to three sets of interrelated assumptions (Stephens and Krebs 1986). Without going into too many details, it is still important to appreciate these sets because they help both to characterise the core of foraging theory, and to understand why this core does not allow for the representation of any selection or evolutionary dynamic. First, *decision assumptions* are certainly those around which most foraging models are initially framed. They account for a particular “decision”—or a particular type of choice—assumed to be taken by an organism. Here, decision or choice have to be understood minimally. Observing an animal picking out particular options, in a non random fashion, among a finite set is sufficient to infer the presence of a decision related to this set of options. As such, no conscious state or rational process needs to be presumed when a phenomenon of this sort is studied using OFT.

In behavioural ecology, a simple and well-known example of decision studied is that of the type and proportion of prey items that should be consumed when several prey types are available (Krebs et al. 1977). For instance, should an animal preferably eat small and abundant prey, or rather ones that are juicier but harder to find? Although it is a limpid example of decision-making, there is no straightforward way to resolve it. It may depend on the exact proportion of the two prey types, on the amount of time available to forage, on the organism's physiological state, and so on. And this is precisely what makes the strength (and the weakness) of foraging models: in order to provide a sound and articulated answer to this question, the problem has to be precisely circumscribed. It's the two other sets of assumptions that allow its contextualisation. In the example above, the choice among prey types has to be framed according to some criterion that allows for the comparison of the available options. The selection of a relevant term of comparison for a particular optimal foraging model falls under the second set of assumptions, the *currency assumptions*. The currency selected for the purpose of modelling is a feature the organism is thought to be maximising (or minimising). Although the models could be of a strictly economical orientation, thus depicting the maximisation of any currency relevant to an organism, biologists seriously narrow down the range of workable currencies, and exploit only those that are assumed to be correlated to

fitness. Hence the vast literature based either on the minimisation of time spent foraging or on the maximisation of energy intake, two organismic features that are a priori assumed to be correlated to fitness in some circumstances.³ Next, in order to be of any use, the model also has to account for those important factors that shape both the decision itself (ex.: the nutritional requirements of the organism; some characteristics of the environment, like the aggregation of prey) and the criteria used to discriminate between options (ex.: the conspicuousness, the abundance or the handling time of each prey types). These are understood as the third set of assumptions, the *constraint assumptions*.

As Stephens and Krebs (1986) clearly show, the three sets of assumptions are closely associated in the model. For instance (their example), the notion of prey type used above implies the forager's capability to categorise its prey into types (a constraint assumption) as much as it shapes the investigated decision, and restricts the types of currency available to the modeller. In the next section, and in order to assess the interweaving of decision and currency assumptions, we look into the rationale behind optimal foraging modelling. This in turn will allow us to assess the link between both sets of assumptions and natural selection, and to demonstrate that OFT is unable to represent dynamics of selection.

Optimal foraging and natural selection

In the previous section, we simply stated that a decision is the making of a choice among a set of options. Whatever the perspective adopted for the appraisal of a particular decision—be it economical, psychological or biological—, it is assumed that the choice made is not a strictly random result, and that it is dependant on both the internal wiring and the environmental context of the organism that takes the decision. Even though they are sometimes envisioned as fulfilling organisms' 'goals', decisions are nothing more than end-products of this dual determination in OFT's framework. When the condition of optimality is added to the process of decision making, it implies that the option retained by the agent is the best of the set according to some currency (assumption 2) and in a particular context (assumption 3). This makes obvious the parallel between optimal foraging theory and decision theory. Indeed, in the field of economics, what is classically assumed to be the best option is the one that maximises utility (Simon 1959). As an example, we might think of a human agent that, having the goal of minimising travelling time (the currency), decides to take the highway instead of the scenic route suggested by travel guides. The agent has options (set by the geography of the region) from which

³ For instance, the minimisation of time spent foraging is *likely* to influence fitness because it leaves more time for other activities such as self-grooming and social interactions. It also modifies the exposure to predation if different activities have different risks (Bautista et al. 1998). Nevertheless, demonstrating a correlation between the minimisation of the time spent foraging and the organism's fitness is not a simple task. As we have underlined in section "Optimality, a multi-use tool", it requires two things: 1° that a variant of the trait of interest is available for comparison; and 2° that some component of fitness (survival, reproductive success or else) is effectively measured. Imagine the technical difficulties that have to be overcome in order to show that a phenotype spending too much time foraging has a lower fitness resulting from missed copulation opportunities, or from a higher predation rate, in comparison to another phenotype that spends less time foraging.

it chooses the one that should best fulfil its goal (that minimise travelling time, and hence maximise utility).

This unsophisticated description of decision theory can be used to analyse optimal foraging modelling. First, and although it is part of the assumptions of the theory, delineating the organism's options is somewhat trivial. Like in decision theory, the specification of the available options is constitutive to model building and, for the model to be tested, these options have to be minimally relevant to the organism. Basically, most pairs of mutually-exclusive motor actions, behaviours or activities could be framed as a decision provided the options they represent are partly determined by the ecological context, and that the hypothesised decision's options are consistently linked together through some period of the organism's life history. Second, foraging theory relies on the definition of a currency in order to appraise the value of the organism's options. In last paragraph's example, travelling time was the currency that allowed comparing the 'highway' and 'scenic route' options. As stated in the previous section, a currency is 1° what links the options open to decision to both the internal wiring and the environmental context of the organism (its "goal" in other words), and 2° a proxy for fitness. Said otherwise, the different foraging options are rated using a variable that is assumed to be correlated to the organism's fitness (Parker and Maynard Smith 1990) *in a particular context*. Typically, it is assumed that net energy intake is a sound proxy for fitness in studies in which the organism's energetic state is crucial for its survival, whether it is to successfully accomplish a migratory flight or to survive through the night during winter (Cuthill and Houston 1997). In such cases, it is fairly easy to model some of the decisions (stay or leave a patch, favour a type of prey among others, walk or fly to forage, etc.) made by the organism given the ecological features it encounters (distribution of food, competition level, predation risk, etc.).

But a currency such as "net energy intake" can also be called upon to model a situation in which survival (or reproductive success) is only remotely at stake. Think of the example introduced earlier in which a bird has to decide what ratio of small and large prey is more profitable in a context where food is aplenty. Said differently, does OFT requires assuming that the currencies it relies on are correlated with fitness whatever the decision looked at, and whatever the ecological context this decision is set in? Of course it does not. For instance, we know all too well that individuals of at least one species can have a "net energy intake" that is detrimental to their fitness: us, humans. The correlation of a currency with the organism's fitness holds in some conditions only. Thus, it is certainly an oversimplification to consider that maximising what is a proxy for fitness in some circumstances amounts to maximise fitness whatever the ecological conditions prevailing (this is the case in Cuthill and Houston 1997). It is worth emphasising this point: the ecological context an investigation is set to explore does not need to be identical to the context in which the correlation between the currency and fitness is demonstrated, or simply assumed to hold. The correlation of fitness with its proxy in a particular context is simply aimed at legitimating the usefulness of the currency in use, not at providing an argument for the immediate fitness 'laden-ess' of all decisions (whatever the ecological context) analysed with OFT using that currency. This subtlety has two main consequences: 1° it considerably broadens the number of decisions that can be investigated using OFT (and the number

of ecological contexts in which some decisions can be looked at); and 2° it casts an interesting light on how OFT relates to natural selection.

Thus, if the observed organism's behaviour complies with the foraging model's description, that behaviour can be said to be optimal. But to the extent a proxy of fitness is used for the purpose of modelling, and to the extent this proxy can be quite remotely correlated to the organism's fitness in the ecological context the study is set in, it cannot be presumed that the optimal behaviour is maximising the organism's fitness. In order to demonstrate that an optimal trait has a positive impact on fitness it must be shown that it has an effect on reproductive success (or any component of fitness), and that this effect would be different if the trait was infra-optimal. Obviously, this sort of information can not be secured with OFT. Fitness assessments require some book-keeping procedure, something that is present in some other optimality modelling (namely, evolutionary game theory) but not in OFT. Likewise, demonstrating the optimality of a particular behaviour is only compatible with the claim that this behaviour has been selected for in the past. It may well be that the foraging decision being investigated has never been selected as such, but that it is rather a fortunate consequence of a string of other evolutionary events. The only way to draw empirical evidences about the evolutionary history of a trait is by comparing the trait (or some of its features) with other 'versions' of it in related extant species—that is through phylogenetic comparisons.

The fact that foraging theory can only provide suggestive indications of natural selection's involvement raises an interesting riddle. Indeed, how can it be vindicated to even try to correlate a currency with the organism's fitness if, as in most cases, the correlation between the currency that is measured and the fitness of the relevant class of organisms cannot be empirically demonstrated? An interesting answer can be drawn from a contemporary reading of McFarland and Houston (1981). Summarily, these authors identify two perspectives on organisms' decision-making. On the one hand, a decision can be circumscribed in a strictly economical way. Looking at the decisions taken in a given context, it is possible to describe what if anything an organism is actually maximising, using any kind of currency. For instance, the decision by a driver to either take the 'highway' or the 'scenic route' needs not be appraised in terms of travelling time. It could also be appraised by using currencies such as the amount of gasoline used, the probabilities of being involved in an accident, the degree of mobile phone coverage along the itinerary, and so on. Expressed mathematically, this description is named an objective function in foraging theory's literature. On the other hand, the same decision can also be looked at in light of the best fit (or the greatest adequacy) it could display to a given ecological context. Although this can be done either in a qualitative or in a quantitative way, here we leave aside the former type since it is essentially based on hunches.⁴ As for quantitatively describing a decision in which the option taken would have the best fit to some environmental features, it amounts to describing the decision that would maximise the organism's fitness given the set of its options and the ecological features these options relate to. Expressed otherwise, the owner of a

⁴ We nevertheless acknowledge its historically determining role in the development of evolutionary thinking, as well as its importance in the preliminary steps of studies using OFT.

“perfectly-fitted-to-its-context” trait would undoubtedly enjoy a higher reproductive success—on average, and everything else being equal—than owners of a less ecologically adequate version of it. This second function is known as the cost function in McFarland and Houston’s vocabulary. It aims at portraying the environmental constraints at play in a particular decision-making process.

Stated schematically, the objective function delineates what an organism does in a given context, whereas the cost function describes what it ought to do in that context if it was perfectly adapted to its environment. Foraging theory is based on the assumption that an objective function *approximates* the cost function it is associated with. It is thus part of OFT’s mechanics to assume that the option the organism takes in a given context is the one it ought to take if the decision-taking process involved was perfectly adjusted to the context. This assumption is critical since it provides the theory with a single and biologically sound variable to optimise for: fitness. In turn, this imposes using only those currencies that can reasonably be thought of as proxies for fitness. Again, whether or not a decision under scrutiny is shown to be optimal, it tells us nothing about its actual contribution to the organism’s future reproductive success, about its fitness. It simply shows that the decision-making process is fitted (adjusted, adapted or adequate) to some of the ecological features it is studied in. It is this *fitness* or *adaptedness* that OFT aims to describe with optimality modelling.

To sum up, it seems appropriate to highlight the two assumptions nested in what is traditionally identified as the *currency assumptions*. First, OFT assumes the objective function (the option effectively taken) is close enough to the modelled cost function (the option that ought to be taken if the decision was perfectly adapted to the context) so the two can usefully be equated. This allows the introduction of fitness—a meaningful variable in biological sciences—as the quantity to be optimised. As we have seen, the decision under scrutiny might significantly impact the animal’s survival and reproductive success only when a fairly narrow set of environmental conditions obtains (during wintertime for some species of bird, for instance). Thus, appraising each option’s hypothetic contribution to the organism’s fitness is a task out of reach in most cases. In order 1° to broaden the number of cases that can be investigated using OFT, 2° to simplify the modelling of the decision, and 3° to be able to test the model’s predictions in the field, a second assumption is introduced. This one supposes that fitness can be usefully replaced by currencies, that is, quantities whose values are correlated to fitness values in at least some ecological contexts. One should not forget or overlook the fact that optimal foraging theory *hypothesises* or *models* an organism as if its behaviour was perfectly adapted to the ecological context in which it is studied. The theory posits a theoretically plausible situation that can be empirically tested. It is not because OFT tests whether or not a trait is maximally adequate (adjusted, adapted, or fitted) to a context that it is also in position to make claims about the trait’s impact on fitness. The two types of statements are certainly related to one another, and there would be much to write about how they relate.⁵

⁵ Fitness as adequacy, adaptation or adjustment of a trait to some ecological feature is of course the first sense in which the term was used in Natural History. Gayon’s (1995) study admirably retraces the history of the term in the period in-between Darwin’s *Origin of Species* and Fisher’s *Genetical Theory of Natural Selection*. This “qualitative” use of fitness has later become coined adaptedness (for instance in

The weak and strong uses of optimality modelling

Having completed our analysis of optimal foraging theory's rationale, it is now time to get back to, and critically appraise, Potochnik's distinction of the weak and strong uses of optimality modelling. As outlined in the introduction, the proposal to distinguish 'uses' in modelling practices rests on the assumption that all optimality models share the property of representing selection dynamics. We have just demonstrated that this is not the case. This, it can be foreseen, will have some consequences on Potochnik's proposal. What exactly these consequences are will be the topic of this paper's final section. For now, we have to highlight the extent to which the distinction of weak and strong uses is relevant to an optimality modelling such as OFT.

In order to analyse Potochnik's proposal, it is useful to state the two related propositions on which it is built:

- P1 The optimisation model represents the selection dynamic that brings about the outcome T.
- P2 Natural selection is the only important evolutionary 'process' that brings about the outcome T.⁶

In the previous section we have shown that P1 is untrue for optimality modelling of the OFT sort. Also, from Potochnik's paper we understand that it is the biologist's position towards P2 that allows to establish whether she intends a weak or a strong use of her optimality modelling. If she commits to P2, her use falls in the 'strong' kind. Otherwise, it belongs to the 'weak' kind.⁷ Here it is important to keep in mind that committing to P2 does not need to be an act of faith. In the context of a particular use of an optimality model able to represent a selection dynamic, it can be a hypothesis submitted to empirical verification at a later stage of the investigation. This is explicit in Potochnik analysis, following that of others (Orzack and Sober 1994a, b).

Now, it is not because P1 is irrelevant to OFT that P2 also is. In fact, it was one of the major goals of Gould and Lewontin's (1979) criticism to denounce the pervasive presence of P2 in most areas of evolutionary biology. Thus, if we consider that users

Footnote 5 continued

Dobzhansky 1950). Also, some people have attempted to articulate adaptedness and fitness in order to provide a definition of the latter, or to provide a formal account of the principle of natural selection (see for instance Brandon 1980; Burian 1983 or Michod 1986).

⁶ Beside the notation, P2 is strictly equivalent to Brandon and Rausher's (1996) proposition S. For reasons different from theirs, we advocate separating claims about the role and importance of natural selection in bringing about an outcome from claims about the locally optimal character of that outcome that are conjunct in Orzack and Sober's proposition O. This makes our analysis of Potochnik's distinction much more intelligible.

⁷ Potochnik (2009) provides the reader with repeated definitions of the weak and strong uses. Here is one representative sample of the way both uses are defined. Weak (p. 189) "The weak use of optimality models upon which I have focused involves the claim that an optimality model accurately represents the actual selection dynamics". Strong (p. 192): "The strong use of an optimality model involves the claim that the model's representation of selection dynamics provides an accurate picture of the important influences on the evolutionary outcome in question."

of OFT can also commit to P2, it could be that Potochnik's distinction is correct whatever the sort of optimality modelling that is being considered. In order to properly assess this possibility, let's define $P1^{OFT}$ so it accounts for what OFT represents.

$P1^{OFT}$ The optimisation model represents the economical dynamic that describes the outcome T.

Here, 'economical dynamics' is simply a generic expression to account for those relations among the trait T, some other feature(s) of the system (traits, ecological factors) and the proxy for fitness being relied on. Using $P1^{OFT}$ now allows us to look at optimal foraging models in light of the distinction between weak and strong uses. Just like in Potochnik's proposal, it is whether or not a biologist commits to P2 that allows to draw the line between the two sorts of uses. To state it plainly, using OFT to investigate a trait, and claiming that natural selection is the most important evolutionary 'process' in shaping that trait would qualify for a strong use of optimality modelling. Thus, it appears that the distinction proposal could indeed hold for the whole family of optimality models, provided statement P1 is given a more general formulation in order to account for the representation of any kind of dynamics.⁸ This restatement could provide philosophers and biologists with a tool to distinguish investigations that commit the sin of adaptationism from those that do not.

Nevertheless, and before we get overenthusiastic with the normative capabilities of this distinction, it is important to assess what are the weak and strong uses of OFT, as outlined above. Indeed, assuming that P2 holds while using OFT does not appear to have the same consequence as when models representing selection dynamics are used. This has everything to do with the kind of dynamics depicted, and with the component on which P2 impinges. While it simply states that the model represents how natural selection produces an outcome, P1 is implicitly modified when P2 is introduced into the investigation. More precisely, the claim that the model represents how a selection dynamic is involved in the production of an outcome—a claim that leaves enough room for other partial explanations of this production, as emphasised by Potochnik—becomes a claim that the selection dynamic depicted by the modelling is sufficient to account for the *evolution* dynamic that produces the outcome. All complementary partial explanations of that production become de facto useless. That is, that natural selection is the only important 'process' that brings about the outcome. Here, what is potentially tainted by P2 is what the dynamic is meant to represent. But, whether the model represents the 'process' of evolution—or more modestly natural selection's part in that evolution—is settled at the same time the model's adequacy is subjected to empirical verification. So, if the model's selection dynamic perfectly fits the naturally occurring changes in a population it is likely P2 is correct in that particular context.

⁸ This could be done using $P1^*$, such as: 'The optimisation model represents a dynamic in which the outcome T is involved', as we will see in section "Neither strong nor weak, but heuristic".

When P2 is introduced into an investigation using optimal foraging theory, $P1^{OFT}$ is modified in a radically different way. What is then tainted by P2 is not what the model's dynamic represents. OFT's dynamics not being able to represent through time intervals, it seems impervious to P2. Rather, what is influenced by P2 is our understanding of 'outcome T'. While this outcome is simply interpreted as a particular decision or trait in $P1^{OFT}$, P2 necessarily adds an evolutionary 'flavour' to it. The trait then is no longer the outcome of whichever 'processes' of evolution, it becomes the outcome of natural selection alone. Said otherwise, 'outcome T' becomes construed as either an adaptation or an adaptive trait. In the two previous sections, we have lengthily shown why and how this is wrong in the context of OFT. Here, what is interesting for the distinction of weak and strong uses of optimality modelling is the fact that whether or not the trait is an adaptation (or an adaptive trait) cannot be decided by empirically testing the model's adequacy. This invites two short remarks. First, committing to P2 can never be empirically grounded *within* OFT's framework. It has to be done by other means. Thus, a strong use of this sort of optimality modelling would instantly qualify as methodological adaptationism. Second, this comes in sharp contrast with the consequence of a commitment to P2 while using an optimality model that depicts a selection dynamic.

Neither strong nor weak, but heuristic

Angela Potochnik's paper aimed to show that the use of optimality modelling can be uncoupled from the thesis of empirical adaptationism (coined P2 in the previous section). In order to do that, she introduced a distinction between weak and strong uses of optimality modelling. This proposal, by way of helping the reader to understand how the *uses* of optimality modelling relate to the 'process' of natural selection, was intended to demonstrate that optimality modelling can be a legitimate tool whether or not P2 is part of the investigation. In fact, P2—which is not strongly supported empirically—does not even need to be endorsed for optimality modelling to be useful. This is an interesting proposal but, as it fails to account for the optimal foraging theory modelling, it needs to be seriously reappraised.

Indeed, leaving aside OFT has two major consequences on the distinction of weak and strong uses of optimality modelling. Firstly, and because P2 cannot yet be definitively ruled out, construing the distinction without OFT implies that P2 is only false in some contexts, based on empirical evidences. Whether or not a model's prediction is met exactly in the natural system under investigation is what determines whether P2 is true or false in that context. Yet, we have seen in the previous sections ("[Optimal foraging theory](#)", "[Optimal foraging and natural selection](#)" and "[The weak and strong uses of optimality modelling](#)") that there is no way P2 can be held in the context of the OFT sort of modelling. Within the strict confines of optimal foraging theory, P2 is always false. And this falsehood is established logically rather than empirically. Thus, a strong use of OFT modelling and a strong use of 'selection dynamics' modelling imply different things.

Secondly, failing to account for OFT in the weak and strong uses distinction dramatically simplifies the complex relations that bind optimality, natural selection and particular investigations. Indeed, OFT and 'selection dynamics' modelling

mobilize the notion of optimality in different ways. While OFT is concerned with optimality at a given point in time, 'selection dynamics' use optimality to make predictions about the changes occurring along a time span, across generations of organisms. Also, the ways the two sorts of optimality modelling depict natural selection also differ dramatically. Even in the context of the weak use, 'selection dynamics' modelling represents natural selection as a 'process' of change in a given natural system. As we have seen above, and as it has been underlined a while ago (Ollason 1987), OFT modelling does not represent natural selection at all. Not directly in any case. As a matter of fact, Potochnik seems to acknowledge that there are some cases in which natural selection is not represented: the investigator uses optimality modelling to garner insights on the traits that 'might have been' or 'could be' used as levers by natural selection.⁹ This is precisely what Orzack (1986) expresses about the case study Potochnik uses to substantiate her analysis of the distinction.

In light of the important consequences that optimality modelling of the OFT sort have on the distinction of weak and strong uses, there are four possible positions that can be held. 1° Dismiss the distinction altogether. This, we believe, would be unfortunate since the basic intuition on which the distinction is built on seems legitimate. Indeed, some optimality modelling such as evolutionary game theory can be used to represent natural selection in the bringing about of a particular outcome; and this representation can in turn be used to make empirically testable claims about the importance of natural selection in the evolution of that outcome. 2° Leave the distinction as it has been introduced. This would preserve the basic intuition, but it would require an important caveat as to why OFT is left aside. 3° Keep the distinction, but take into account OFT by acknowledging the different dynamics represented in the broad family of optimality modelling. This could be done by adopting a more general formulation of P1, such as P1* (introduced in note 8, see below).

But this merely allows the framing of the difficulties outlined at the beginning of this section. Indeed, statements about strong uses would have to be further qualified since they imply different things whether 'selection dynamics' or OFT modelling are considered. Either the statement can be associated with some empirical test, or it is simply logically false. Of course, statements about weak uses would indirectly suffer from this ontological difficulty (to what extent is it legitimate to distinguish weak uses of OFT when all strong uses of that sort imply false statements?). If we turn a blind eye on this problem, the 'weak uses' could still be delineated by the fact that they do not endorse P2. But having adopted P1*, this would mean that whether or not an optimality model represents natural selection is no longer relevant for the distinction of weak and strong uses. This does not seem to be the most satisfactory option in order to progress towards a better understanding of scientific modelling and practices.

⁹ The clearest hint about this is the following sentence (pp. 188–189): "There is another common use of optimality models that is still weaker: optimality models are also used to develop and explore adaptive hypotheses at preliminary stages of investigation, when little is known about the evolutionary factors at work. Used in this capacity, the aim of optimality modelling is merely to represent possible selection dynamics, and the standards for success are correspondingly lower."

This leaves us with a last possible position about what could be done with Potochnik's distinction of weak and strong uses: 4° Reshape the original distinction and subordinate it to a second, more fundamental distinction. This would allow the introduction of a third class of optimality modelling uses, the heuristic uses. As we envision it, the tripartite distinction could be stated using a set of three propositions (original proposition numbers are kept for the sake of clarity):

- P1* The optimisation model represents a dynamic in which the outcome T is involved.
 P^{new} A selection dynamic is directly represented in the optimisation model.
 P2 Natural selection is the only important evolutionary 'process' that brings about the outcome T.

Framed in this way, whether or not P^{new} holds would allow to distinguish 'weak' or 'strong' uses from heuristic uses (those uses that provide insights on the levers possibly used by natural selection). Then, it is whether P2 is empirically verified (or simply held by an investigator) that would allow the discrimination between 'strong' and 'weak' uses. We are confident that this tripartite framework would give a fuller understanding of the practice of optimality modelling in biological sciences. While it would still account for Potochnik's original intuition about scientists' statements on the importance of natural selection in bringing about an outcome, it would also provide a criterion to identify those optimality modelling that describe dynamics in which a trait is involved, and thus can provide insights about features on which natural selection could operate (or could have been operating).

Conclusion

In this paper, we aimed to show that Potochnik's distinction is grounded on a too narrow understanding of what is optimality modelling. Indeed, it does not account for the models used in optimal foraging theory. Interestingly though, this shortcoming is not fatal for Potochnik's original suggestion. The distinction of weak and strong uses simply needs to be better circumscribed, and more importantly to be stated in a way that accommodates a third sort of uses: the heuristic uses. Indeed, this addition appears necessary for claims about the whole family of optimality modelling to be legitimate. Otherwise, the distinction's scope could be too limited and hence of a rather disappointing usefulness.

Our addition to Potochnik's distinction is proposed with two intents in mind. To begin with, the tripartite distinction we advocate for could allow a better delineation of what has become known as adaptationism and types of adaptationism. Indeed, we have shown that claims about the predominant importance of natural selection in bringing about an outcome (P2) have different consequences whether they are made in the context of 'selection dynamics' (i.e. evolutionary game theory) or OFT modelling. This is made obvious if we consider how P2 impinges on our representation of the model's dynamic: on the dynamic itself, or on the dynamic's outcome. It thus appears that two types of adaptationism—empirical and methodological (Lewens 2009)—could be relevant categories when one both probes into the

practice of optimality modelling, and carefully assesses what scientists say about their own work. In line with this, the tripartite distinction could also cast an interesting light on the influence of Gould and Lewontin's *Spandrels* paper. This could be done by testing whether or not biologists using optimality models have been less prone to advocate or defend P2 after the *Spandrels*' publication; and whether or not the fact that they used 'selection dynamics' or OFT modelling made any difference.

As a concluding remark, we cannot help but to express our puzzlement about the fact that an important number of philosophy papers dealing with optimality modelling have been exclusively concerned with evolutionary game theory. Although there are some notable exceptions (Beatty 1980), discussions about whether or not the thesis of adaptationism can be verified barely allude to optimality models such as those used in optimal foraging theory (Orzack and Sober 1994b; Brandon and Rausher 1996; Orzack and Sober 1996). Arguably, accounting for this sort of modelling might have had little impact on the core of this very interesting debate. Nevertheless, it could have made obvious that any discussion about adaptationism should take into account the sort of formalism being used, the hypotheses scientists intended to test, and the claims they make following such testing.

Acknowledgments This paper has greatly benefited from the constructive criticism of three anonymous referees for *Biology and Philosophy*, and from all those precious exchanges with members of the Biogéosciences (Dijon) and Laboratoire de Biométrie et Biologie Evolutive (Lyon 1) labs. Many thanks to P. Monfils for her efficient spellchecking. J.-S. Bolduc was supported financially by the Fonds Québécois de Recherche sur la Société et la Culture (FQRSC).

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