

Adaptive walks on behavioural landscapes and the evolution of optimal behaviour by natural selection

MARC MANGEL

Zoology Department and Center for Population Biology, University of California, Davis, Ca 95616, USA

Summary

One of the main challenges to the adaptationist programme in general and to the use of optimality models in behavioural and evolutionary ecology in particular is that natural selection need not optimise fitness. This challenge is addressed by considering the evolution of optimal patch choice by natural selection. The behavioural model is based on a state variable approach in which a strategy consists of a sequence denoting the patch to be visited as a function of the organism's state and time. The optimal strategy maximises expected terminal reproduction. The fitnesses of alternative strategies are computed by iteration of the associated equations for fitness; this characterises the adaptive behavioural landscape. There may be enormous numbers of strategies that have near optimal fitnesses. A population model is used to connect frequencies of behavioural types from one generation to the next. Theories on adaptive walks on fitness landscapes are considered in the context of behaviour. The main result is that within the context of optimality arguments at selective equilibrium, sub-optimal behaviours can persist. General implications for research in behavioural ecology, including tests of behavioural theories, are discussed.

Keywords: Optimality, behaviour, adaptive landscapes, evolution

Introduction

Among the main challenges to the 'adaptationist programme' (Gould and Lewontin, 1979) and to the use of optimality models in biology, and in behavioural and evolutionary ecology in particular, are the assertions that natural selection does not optimise fitness and that organisms are so constrained by structure (e.g. neurobiology, developmental constraints, correlations among traits) that they may not be able to obtain optimal solutions, however such solutions are defined. This paper and Mangel (1990) are attempts to answer these challenges, using behavioural modelling as an example. A third challenge is that a genetic mechanism for attaining optimality may not exist. The volume edited by Loeschcke (1987) contains a set of papers that address this question from the perspective of quantitative genetics. Charnov (1989) recently approached it beginning with Fisher's fundamental theorem.

Optimality arguments often form the theoretical foundation in behavioural ecology, as for example in optimal foraging theory (see Krebs and Davies, 1984; Stephens and Krebs, 1986; Mangel and Clark, 1988). Such arguments are based on the implicit assumption that a population consists of individuals who carry repertoires of behaviour and can select the 'optimal' behaviour according to the demands of the local ecology and the organism's physiology. These are 'open' behavioural programmes (Mayr, 1974). The alternative assumption is that a population consists of repertoires of individuals, each with genetically fixed behaviour ('closed' behavioural programmes) and that natural selection changes the distribution of repertoires from one

generation to the next. The former assumption is the foundation of optimal foraging theory and its generalisations and the latter assumption is at the heart of population genetics. In this paper, I want to study the connection between these assumptions and moreover analyse the implications for behavioural ecology.

In recent years, the foundations of the adaptationist programme have been investigated, criticised and defended (Oster and Wilson, 1978; Gould and Lewontin, 1979; Dennett, 1983; Mayr, 1983; Mitchell and Valone, 1990). In behavioural ecology, because of an emphasis on optimal foraging theory, there has been considerable interest. Yet even the strongest critics (Gray, 1987; Pierce and Ollason, 1987) and proponents (Stephens and Krebs, 1986) have missed a key point: within the context of optimality arguments at selective equilibrium, sub-optimal behaviours can persist over time*. That is, in addition to all of the other reasons commonly given as to why animals might not be able to achieve 'optimal' solutions (Gray, 1987, p. 71ff; Pierce and Ollason, 1987), the standard framework of optimality thinking, augmented by a few concepts from population biology, shows that the persistence of non-optimal strategies is to be expected. The implications of this point for testing behavioural models (Stephens and Krebs, 1986, Chapter 9) are enormous because it shows that we must focus on the values of predicted behaviours as well as the predicted behaviours themselves. This means that empirical tests based on a 'yes' or 'no' response are insufficient and that regardless of the outcome of the experiment we must focus both on behaviours and the values (i.e. fitness) of those behaviours.

In order to expand these ideas, I consider the adaptive landscape of patch selection, as described in Mangel and Clark (1986; 1988). In the next section, I summarise that model of patch selection and show how it leads to an adaptive behavioural landscape. In the third section, I incorporate models of population genetics and in the fourth section explicitly consider adaptive walks (Kauffman and Levin, 1987; Macken *et al.*, 1990) on the behavioural landscape. In the last section, I discuss the implications for behavioural ecology.

The adaptive landscape for patch selection

Patch Selection Model

During each period of a non-breeding interval of length T , an organism must choose one of H patches in which to feed. Patches vary in productivity and predation risk; this variation is assumed to be known to the organism. At the end of the non-breeding interval, all the organisms that have survived reproduce. Elaborations of this model (e.g. stochastic end time, unknown patch parameters, incremental reproduction) can be found in Mangel and Clark (1988).

The state of the organism at time t is measured by energy reserves $X(t)$. There is a critical level x_c such that if $X(t)$ falls below the critical level the organism is dead and a maximal level x_m that is an upper bound to $X(t)$. The i^{th} patch is characterised by

$$\begin{aligned} \lambda_i &= \text{Prob \{finding food in the patch in a single period\}} \\ Y_i &= \text{Energetic value of the food found in the patch} \\ \alpha_i &= \text{Energetic cost per period of foraging in the } i^{\text{th}} \text{ patch} \\ \beta_i &= \text{Prob \{predation in the patch in a single period\}} \end{aligned} \tag{1}$$

At time T , terminal fitness is a function $R(X(T))$. Since no reproduction occurs before T , the key components of fitness are survival (i.e. avoiding both starvation and predation) during the non-breeding period and terminal reproduction at T . Hence, optimal behaviour is defined to be the

*This is more complex than simply stating that the vicinity of the peak of a function $f(u)$ is relatively flat (because $f'(u) = 0$ at the peak). For example, Mangel and Clark (1988, p. 188) discuss the non-robustness of optimal decisions. To answer the challenge concerning the evolution of optimal behaviour by natural selection, one must address the temporal change of frequencies of non-optimal strategies.

sequence of patch visitations, as a function of time and reserves, that maximises expected terminal fitness. This fitness is

$$F(x, t, T) = \max E\{R(X(T)) | X(t) = x\} \quad (2)$$

In this equation, the maximum is taken over feasible behavioural decisions; i.e. which patch to visit for each period between t and $T-1$ and $E\{ \}$ denotes the expectation over the stochastic events of finding food and avoiding predation. The lifetime fitness function $F(x, t, T)$ satisfies the following equation (Mangel and Clark, 1988)

$$F(x, t, T) = \max_i \{ (1 - \beta_i) [(1 - \lambda_i) F(x'_i, t+1, T) + \lambda_i E(x''_i, t+1, T)] \} \quad (3)$$

where $x'_i = \text{chop}[x - \alpha_i; x_c, x_m]$, $x''_i = \text{chop}[x - \alpha_i + Y_i; x_c, x_m]$ and $\text{chop}[z; a, b] = a$ if $z < a$, b if $z > b$ and z otherwise.

Equation 3 is solved 'backwards' in time, for t ranging from $T-1$ to 1 in steps of -1 . The condition $F(x, T, T) = R(x)$ acts as an initial condition for the solution. Computational algorithms for the solution of Equation 3 are described by Mangel and Clark (1988). As Equation 3 is solved for fitness, one also generates the optimal strategy, which is the sequence of patches to visit. This optimal strategy is denoted by $i^*(x, t)$, i.e. the patch that should be visited in period t if $X(t) = x$. Often this strategy will be unique in that for a given set of patch parameters there is only one choice of i for each x and t that maximises the right hand side of Equation 3. The fitness associated with the optimal strategy will be denoted by $F^* = F(x_m, 1, T)$.

The optimal strategy S^* is a 'list' of patches to visit over time and physiological space, in the same way that a protein or nucleic acid can be represented by a linear sequence (Macken *et al.*, 1990). Here, I choose to represent this sequence as

$$S^* = \{ i^*(x_c+1, T-1) i^*(x_c+2, T-1) \dots i^*(x_m, T-1) i^*(x_c+1, T-2) \dots i^*(x_c+1, 1) \dots i^*(x_m, 1) \} \quad (4)$$

As a numerical example, consider a three patch environment in which $\alpha_i = 1$ in every patch and the other patch parameters are as follows:

Patch	λ	Y	β
1	1	0	0
2	0.4	3	0.002
3	0.6	5	0.04

Patch 1 is safe ($\beta=0$) but also non-productive ($Y=0$) and patches 2 and 3 are risky ($\beta's > 0$) but productive ($\lambda_i Y_i > 0$). Other parameters are $x_c = 3$, $x_m = 6$, $T = 10$ and $R(x) = 1$ if $x > x_c$. In this case, the optimal strategy, determined by the solution of Equation 3 is unique and is given by the list

$$S^* = \{ 3 1 1 3 3 1 3 3 3 3 2 3 3 2 3 3 2 3 3 2 3 3 2 3 3 2 \} \quad (5)$$

This is the optimal strategy, as a function of time and physiological state.

Behavioural landscape

The adaptive behavioural landscape is generated by considering alternative behavioural strategies. An alternative strategy S consists of a modification of the list given in List 5. Animals with alternative strategies respond to state variables (reserve level) using behaviours (patch choice) different from animals with the optimal strategy. These different strategies, denoted generically by S , are also lists. For example, an alternative strategy might be

$$S = \{ 3 1 2 3 3 2 3 3 3 3 2 3 3 2 3 3 2 3 3 2 3 3 2 3 3 2 \}$$

in which the italic numbers show that patch 2 is visited instead of patch 1 when the reserves are x_m in periods $T-1$ and $T-2$.

Alternative strategies have associated fitnesses computed by an equation similar to Equation 3. Let

$$F(x, t, T|S) = E\{R(X(T)) | X(t) = x \text{ and strategy } S \text{ is followed}\} \quad (6)$$

No optimisation step is needed in the Equation that $F(x, t, T|S)$ satisfies, since the strategy is specified:

$$F(x, t, T|S) = \{1 - \beta_{i(x,t)}\} [(1 - \lambda_{i(x,t)}) F(x_{i(x,t)'}, t+1, T|S) + \lambda_{i(x,t)} F(x_{i(x,t)''}, t+1, T|S)] \quad (7)$$

The end condition for Equation 7 is the same as the end condition in List 5 and $F(x, t, T|S)$ is computed in a similar fashion. We can then define a fitness for strategy S by

$$F(S) = F(x_m, 1, T|S) \quad (8)$$

Strategies $S = \{i(x, t)\}$ that differ from the optimal strategy $S^* = \{i^*(x, t)\}$ can be called 'alternates'. An ' n -step alternate' has $i(x, t) = i^*(x, t)$ except for n values of (x, t) at which $i(x, t)$ takes a value different from $i^*(x, t)$. In this case, it is helpful to index strategies by the number of differences, and the location of the differences, from the optimal strategy. Thus, a strategy $S_1(z, h)$ differs from the optimal in that at position z in the list, the optimal patch choice is replaced by h and a strategy $S_2(z_1, h_1; z_2, h_2)$ differs from the optimal strategy at positions z_1 and z_2 . This process generates an adaptive landscape for patch selection, by considering strategies that differ from the optimal at an increasing number of positions and computing the fitness of each of those strategies.

For the numerical example there are about 50 one step alternates, 3000 two step alternates and 155 000 three step alternates. The fitness of these different alternates can be measured relative to the optimal fitness. Some of the alternates may have fitness close to optimal (Gladstein *et al.*, 1989, provide another example of this phenomena). For example there are nearly 1000 three step alternates with fitness between 99.8 and 99.9% of optimal. Of course, there are many alternates with fitness less than 99% of optimal (152 734 of the three step alternates, to be precise) and selection will rapidly eliminate these.

Behaviours with fitnesses that are very close to optimal may persist for a long time. The central question is how such persistence is computed and what it means for the evolution of optimal behaviour.

Mutation–selection balance and the lesson from population genetics

Suppose that individuals are born with a fixed patch visitation strategy; however, during reproduction, a strategy may not be replicated exactly. The cause of the lack of perfect replication might be mutation, segregation or a variety of other genetic mechanisms. The detailed nature of these mechanisms is not important here, but they will generally be called 'mutation'. Assume that the probability that a strategy is reproduced true in the next generation is $1 - \rho$. If an untrue reproduction only leads to a difference of a single entry of the strategy, then individuals produce offspring that are at most one mutational step away from themselves.

The processes in the population dynamics are survival, and reproduction (during which 'mutation' may occur), followed by allocation of resources to offspring. Survival depends upon the strategy that an individual carries, as described in the previous section. The individual with strategy S produces two types of progeny: $RF(S)(1 - \rho)$ offspring with strategy S and $RF(S)\rho$ offspring with different strategies. The precise distribution of the different strategies after

reproduction depends upon the nature of the mutations during reproduction. In the simplest case, the allocation of resources to offspring can be viewed as a random process, subject to the constraint of a carrying capacity. That is, if the total number of individuals in any generation is less than an environmental carrying capacity N_T , reproduction is assumed to be density independent. Otherwise, strategies are allocated resources in proportion to their numbers after reproduction.

These assumptions lead to a population genetic model involving 'mutation-selection' balance. That is, genetic equilibrium will be characterised by a *frequency or probability distribution of strategies*, rather than by a single strategy (Turelli, 1984). We are particularly interested in the properties of this equilibrium distribution of strategies (will the strategy corresponding to the optimal behaviour predominate?) and the rate at which this distribution is approached (if it does predominate, how long will it take to do so?). Formal mathematical analysis of this model leads to the following conclusions, which are consonant with standard theories of population genetics (Futuyma, 1986).

The stationary or equilibrium distribution of strategies need not be sharply peaked at the optimal strategy; alternates with fitness nearly optimal may have considerable probabilities of presence. Let $p^*(k)$ denote the fraction of optimal strategies present in generation k and p_{eq}^* denote the fraction at equilibrium (i.e. the limit of $p^*(k)$ as $k \rightarrow \infty$). The stationary distribution can be characterised analytically, at least for small values of the mutation parameter ρ .

Even when the optimal strategy ultimately predominates, in the sense p_{eq}^* is approximately equal to 1, the rate at which $p^*(k)$ approaches p_{eq}^* should be considered. The rate of evolution of p^* is initially the same over a wide range of values of ρ , even though the ultimate value of p_{eq}^* differs considerably. The time dependence of $p^*(k)$ usually must be determined by numerical solution of the dynamic equations characterizing $p^*(k)$.

Even if p_{eq}^* ultimately approaches 1, the time for the optimal strategy to predominate (say $p^*(k) = 0.05$ or 0.75) may be considerable. In particular, this time may greatly exceed the time scale on which the environment changes. Since environmental changes will change patch parameters, an environmental change may lead to the currently optimal strategy no longer being optimal and a one, two or multi-step alternate becoming the new optimal strategy.

Thus, evolutionary arguments in behavioural ecology cannot be based on the length scale of the geological record. Rather, they must be based on the length scale of the constancy of the local environment. These may be difficult to infer from the geologic record. For example, selection pressures on foraging in Galapagos finches have been shown to vary from year to year (Grant and Grant, 1989).

Adaptive walks on behavioural landscapes and sub-optimal peaks of fitness

Recent work on adaptive walks on fitness landscapes (Gillespie, 1984; Kauffman and Levin, 1987; Macken *et al.*, 1990) has concentrated on the evolution of proteins and the immune system. However, much of the theory can be applied to behavioural problems. Typically the theories have three main assumptions (Macken *et al.*, 1990). First, mutations involve only a single change in a sequence, i.e. the mutations are one step mutations. Second, mutations are expressed only if the mutation has higher fitness than the original molecule. Third, when an alternate has higher fitness, all original molecules will be replaced by the alternate. These three ideas can be traced at least to Haldane (Provine, 1990). Macken *et al.* (1990) discuss alternative assumptions and their importance. Perhaps the most important feature for such a walk on an adaptive landscape is that

the walk can be 'trapped' at sub-optimal peaks of fitness. That is, at some stage in the evolution, none of the one-step alternate neighbours have higher fitness than the current strategy. The implication for behavioural problems is that a sub-optimal strategy for patch selection may predominate. On the other hand, as described in the previous section, the adaptive walk on a behavioural landscape may not necessarily meet the second and third assumptions. That is, there is no reason to assume that one step alternates with lower fitness than the current strategy, but which are intermediate to a multi-step alternate with higher fitness will not be expressed. As long as $F(S)$ is greater than 0, a strategy will be present in the next generation. In addition, for behavioural problems in which the time for selection is the same as the lifetime of the organism, it is clearly not true that when an alternate of higher fitness is found (even if it is the optimal strategy), then all other alternates of lower fitness are instantly replaced. The time scales of protein synthesis and lifetime reproduction are sufficiently different that a valid assumption in one model might be questionable in another. The net effect of weakening the second and third assumptions listed above is a prediction again consonant with the results of the previous section: strategies with sub-optimal fitness may not only be present, but depending upon the assumptions of the adaptive walk, may even predominate.

Implications for behavioural ecology

Because of the dominance of Popperian thinking in science, there is always an immense pressure to 'test by falsifying' a proposed theory. Alternatives to the Popperian view might be more appropriate (Polanyi, 1962; Rhodes, 1988, pp. 31–5; Mitchell and Valone, 1990) (this is a subject for a separate article). Consequently some recent work has focused on testing predictions of behavioural theories and, in particular, 'optimal foraging theory (OFT)'. We can consider, for example, the tests of OFT by Stephens and Krebs (1986, Chapter 9) and Gray (1987, p. 76 ff). Gray reviewed nearly 100 empirical papers on diet choice and compared the results with the four main predictions of that theory, namely, individuals should: (a) select profitable prey; (b) be more selective when profitable prey are abundant; (c) ignore prey outside the optimal diet,

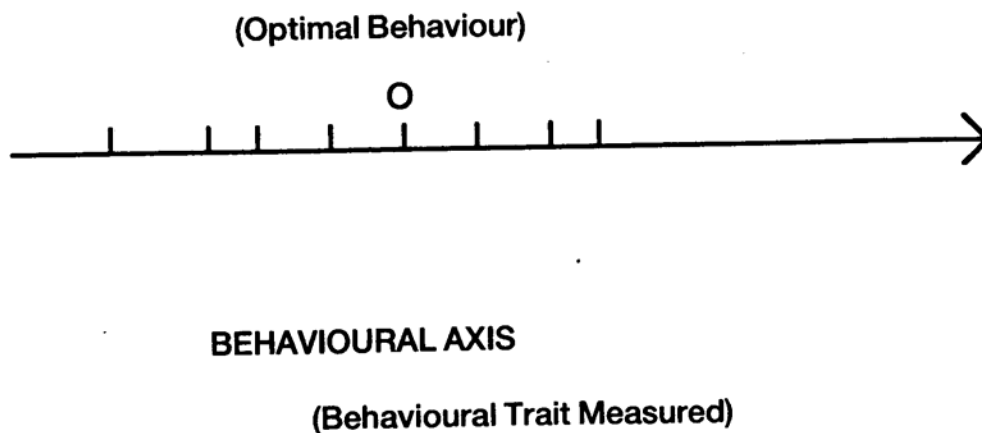


Figure 1. The implicit world view used in most tests of optimality models. A 'behavioural' axis is created and the optimal behaviour is a 'point' O on this axis. Deviations from optimal, as shown by vertical lines then 'disprove' the optimality argument. The behavioural axis is typically some kind of trait such as diet composition, prey load taken by a central place forager, or super-parasitism by a parasitoid.

regardless of their abundance; and (d) not exhibit partial preferences. In his study, Gray reports the kind of study (laboratory or field), the result of the study (whether the prediction was supported, indecisive, or not supported), and quantitative aspects of the study. Gray found moderate support (in 47 out of 86 studies prediction (a) was supported) to poor support (prediction (d) was not supported in any of 44 studies) for the theory. Stephens and Krebs (1986, p. 187 ff) report on the results of more than 100 studies of tests of the models of diet choice, patch selection, or central place foraging. They too find a range of results, from quantitative agreement with the model to observations that are inconsistent with the model. All of the models being tested involve an identification of fitness with rate of energy gain and thus optimal behaviour with maximal rate of energy gain.

These tests have an implicit world view in which one tests the theory with a 'behavioural' axis (Fig. 1). That is, one somehow describes a possible range of behaviours along a continuum and then places the observations on this continuum. The typical result might be: one of seven organisms behaved optimally (e.g. did not exhibit partial preferences), so the optimality model is rejected. Since real organisms are constrained by physiology, state variables (Mangel, 1989) may explain much of the inconsistencies (e.g. partial preferences – see McNamara and Houston, 1987; Mangel, 1989). However, none of these tests actually report the fitness of sub-optimal strategies. For example, rate maximisation formulations (Mangel, 1989) usually predict 0/1 decisions without regard to how close the rate of energy gain with the '0' decision is to the rate of energy gain with the '1' decision. If these are close, as they often will be (Mangel, 1989, provides some examples for the rate of offspring production by parasitoids), then sub-optimal strategies can persist for at least as long as the career of a typical investigator. For example, suppose that accepting only the superior prey type gives an energy flow of 0.19. We would expect quite different behaviours if accepting both prey types gave an energy flow of 0.17 in one case and 0.03 in another case.

Put another way, the work developed in this paper has two main implications. First, when a population is 'randomly' sampled for behavioural phenotypes, there may be a considerable proportion of non-optimal phenotypes in the population. The proportion of non-optimal individuals will depend upon the rates at which alternate behavioural sequences are produced, the relative fitness of the non-optimal strategies, and the constancy of the environment. It is thus insufficient, for example, to claim that 'optimal foraging theory fails' because one tests an organism and finds that its behaviour deviates from the behaviour predicted by optimality arguments. That is, as it is traditionally viewed, optimal foraging theory (OFT) makes no allowance for sub-optimal strategies at all (no variance at equilibrium). Thus, any detected variation 'disproves' traditional OFT. The work reported in this paper suggests a natural source of variation; state variables and behaviour on a fitness landscape. In addition to assessing the behaviour, the fitness associated with that behaviour must be assessed. Fluctuating environments are likely to enhance the mixture of behavioural phenotypes, since a strategy that was optimal last year need not be optimal this year. Second, tests of optimal foraging theory that are based on an arbitrary fitness function such as rate of energy maximisation must be considered very carefully, regardless of their outcome. It is imperative to attempt to understand the structure of the fitness function and its associated trade-offs. That is, instead of working solely along a 'behavioural' axis (Fig. 1), we must work in a plane comprised of both 'behavioural' and 'fitness' axes (Fig. 2). This point is beginning to be recognised by empirical workers. For example, Janssen (1989, p. 478) writes: '. . . it seems very important to compare the fitness gain of the optimal strategy to that of alternative strategies'. That is, a major role of optimality models is to guide our thinking about the role and kind of selective forces operating in the system.

The task for both experimentalists and theoreticians, then, is to develop indices that can be

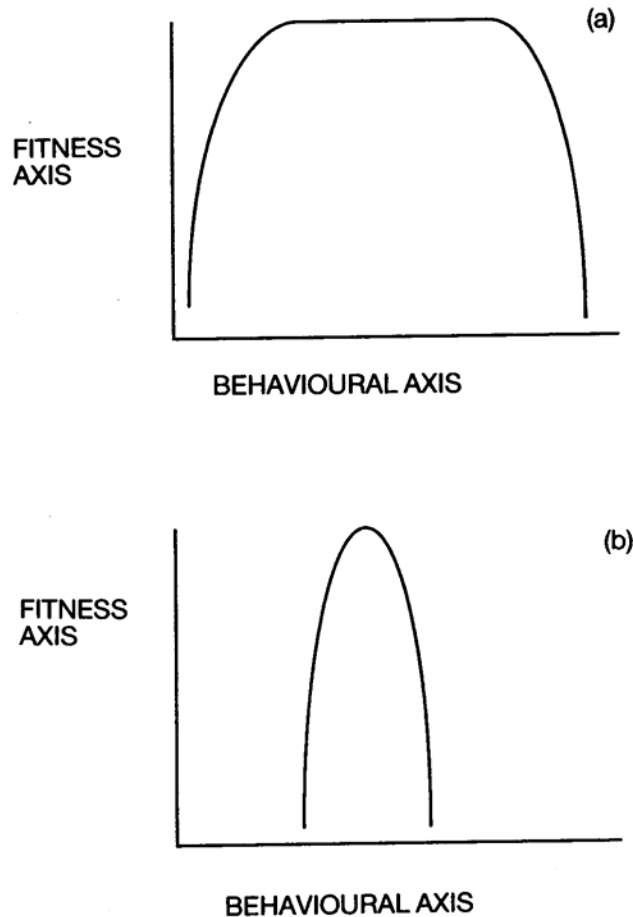


Figure 2. An alternate world view in which we deal with both a 'behavioural' axis and a 'fitness' axis. For panel (a), at selective equilibrium we anticipate a large number of non-optimal strategies to persist while for panel (b) the range of persistent non-optimal strategies would be much smaller. The implications of observations similar to those in Fig. 1 are that rejection of the optimality argument would be more cogent in case (b) than in case (a).

used to determine whether the behavioural/fitness plane is as in Fig. 2a or Fig. 2b. For example, suppose that F^* is the theoretically computed optimal fitness and F_{obs} is the fitness of the observed behaviour. An appropriate statistic might be $(F_{\text{obs}}/F^*)^\tau$ where τ is a characteristic time scale for the environment. In the example provided above, we have $F^* = 0.19$ and $F_{\text{obs}} = 0.17$ or 0.03 ; suppose $\tau = 1$. In the first case, the statistic would be 0.89 and in the second case it would be 0.16 . Clearly non-optimal behaviour corresponding to a fitness ratio of 0.89 would have different persistence, and implications for the optimality model, than non-optimal behaviour corresponding to a fitness ratio of 0.16 . As a historical footnote, when operations research was first developed in this country (Morse and Kimball, 1952), the workers introduced the concept of a 'hemibel', which is the logarithm of 3. They felt that if the theoretical optimal value of an operation and its observed were within a factor of three of each other, then there was little that analysis could do to improve the operation. In evolutionary ecology, we are able to control experiments more finely

and thus can hope to get closer than one hemibel difference between theory and observation. We should, however, not be fixated on point optima.

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