Optimality theory in evolutionary biology

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Optimization models help us to test our insight into the biological constraints that influence the outcome of evolution. They serve to improve our understanding about adaptations, rather than to demonstrate that natural selection produces optimal solutions.

In recent years, optimization theory and game theory have been widely used, particularly by field biologists, to analyse evolutionary adaptation[1-7]. During the same period, originating with a classic paper by Gould and Lewontin[8], there has been continuing criticism of the optimization approach. This criticism seems to arise from the idea that those who adopt the approach assume either that animals and plants are optimally adapted, or that they are trying to prove that they are so. Hence any demonstration of the role of chance events—for example, that much molecular variation is selectively neutral, or that unpredictable events have had a major effect on evolution—has been seen as undermining the optimization approach. If, by this review, we could lay rest to the idea that the application of optimization theory requires either that we assume, or that we attempt to prove, that organisms are optimal, we would be well satisfied.

It is true that the optimization approach starts from the idea, already familiar to Darwin, Wallace and Weismann in the last century, that adaptation is a pervasive feature of living organisms, and that it is to be explained by natural selection. It is not our aim to add to this the claim that adaptation is perfect. Rather, the aim is to understand specific examples of adaptation, in terms of the selective forces and the historical and developmental constraints operating. This requires that we have an explicit model, in each specific case, that tells us what to expect from a given set of assumptions. The predictions are an inevitable consequence of the assumptions. A model cannot then be 'wrong' (unless analysed incorrectly), but it can certainly be inappropriate if it is based on assumptions that are not well founded.

We distinguish between general models and specific models[9], though in reality they form part of a continuum. General models have a heuristic function; they give qualitative insights into the range and forms of solution for some common biological problem. The parameters used may be difficult to measure biologically, because the main aim is to make the analysis and conclusions as simple and direct as possible. Specific models are designed to be applied quantitatively to particular species, and include parameters that can readily be measured. They are often modified (and more complex) versions of some general model, devised specifically for comparison with a particular set of observations. If the predictions of the model match the biological observations, we may hope that we have made correct assumptions about the nature of adaptations.

Evolutionary optimization models

The optimality approach involves the construction of a model about adaptation. First, it is necessary to ask an explicit biological question, which may be general (for example, why is the sex ratio often unity?[10-12]) or specific (for example, why do dungflies copulate for 36 minutes?[13]). If we do not know that the sex ratio is often unity, or that dungflies copulate for 36 minutes, then the equivalent questions might become: what sex ratio is the most likely to result from natural selection? and how long should dungflies copulate as a result of male–male competition? Either way, the question is assumed to have an adaptive answer, otherwise we cannot proceed to establish whether a given adaptive process can generate the correct solution.

Next, a range of alternative actions or 'strategies' relating to the question is defined. For the question about sex ratios, the obvious strategy set (the range of phenotypic variants) to consider is all points in the continuum from producing only male offspring to producing only female offspring. But strategy sets need not be continuous: many models involve discrete strategies. Thus, for a bird's choice of where to nest, alternative strategies might include nesting in a tree or nesting on the ground.

The strategy set simply specifies the plausible alternatives, given what we consider it possible for evolution to achieve. Often, as in the case of sex ratios, there is a simple and obvious strategy set that logically covers all the possibilities. But in other cases it is necessary to rely simply on biological intuition. Some feel for candidate strategies can often be obtained from the existing range of variation. Typical biological constraints usually define some obvious boundary conditions for the strategy set, but strategic possibilities that have never in fact been observed are included unless there are reasons of this kind for leaving them out.

In the construction of the model an assumption must be made about what is being maximized, and some measure of darwinian fitness is usually used. The simplest direct criterion is the expected lifetime number of surviving offspring produced by an individual pursuing a given strategy ('individual fitness'), defined in units of generation time (which may vary with phenotype). Many life-history theorists prefer to use the more cumbersome rate of increase per individual (r, the solution of the Euler–Lotka equation[14]). But in most circumstances, the relative reproductive outputs of different strategies (which equate roughly with the selection coefficients used in classical population genetics) will suffice. When interacting individuals are relatives, however, it is more satisfactory to use Hamilton's 'inclusive fitness'[15], which sums, for an allele prescribing a given strategy, the aggregate consequences for that allele (inclusive of the same allele carried in relatives). Other non-darwinian criteria such as group selection (the notion that selection minimizes the extinction rate of local groups[16]) and species selection (the idea that adaptation is best explained in terms of differential extinction of species[17]) have their advocates, but (with good reason) are not currently popular in most adaptive contexts.

The optimization criterion is often an indirect measure of fitness. For example, when analysing animal gaits, Maynard Smith and Savage[18] assumed that energy expenditure at a given speed would be minimized (or conversely, that speed for a given energy expenditure is maximized). In the case of animals foraging for food, it is often assumed[5] that natural selection will maximize the net rate of energy intake, with the number of offspring (fitness) increasing with total calorific intake over a long period of foraging. Sometimes it is assumed that fitness is directly proportional to the indirect criterion used: however, this will often not be so, and nonlinearity may affect the quantitative predictions of the model (see Box 1.4).

Once the optimization criterion has been chosen, assumptions have to be made about the fitness consequences (or 'payoffs'—a term borrowed from game theory[2,19]) of the different strategies, which may involve construction of mathematical models.

Payoffs are expressed in units of the criterion to be maximized, and are thus direct or indirect measures of fitness. They often

BOX 1 **Some examples of simple (frequency-independent) optimization**

(1) Benefits B or costs C of adopting strategy x. For the case of the foraging lapwing, $B(x)$ is the calorific value of prey items obtained after each move of distance x, and $C(x)$ is the energetic cost of moving distance x. For reasons discussed in the text, we expect $B(x)$ to increase to its asymptote by the stage where the movement distance equals the diameter of the circle of perception (this function can readily be formulated explicitly), and we expect $C(x)$ to be linear increasing.

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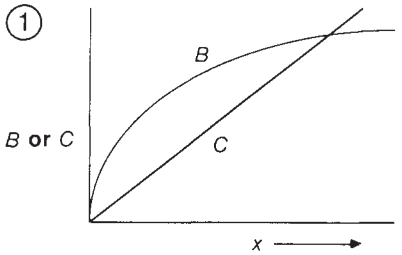

(2) The indirect fitness function. The proposed optimization criterion is the net energy gain per move, E. This is $E(x) = B(x) - C(x)$. The best movement distance, x^*, is that which maximizes E. It therefore has

$$\frac{dE(x)}{dx} = 0$$

and satisfies

$$\frac{d^2E(x)}{dx^2} < 0$$

in order that x^* is a maximum, not a minimum. This gives $B'(x^*) = C'(x^*)$; that is, the optimal movement distance occurs when the gradient of the benefit function drops to the same value as the gradient of the cost function. Biologically, the lapwing should continue to move until the marginal benefits from the next step become equal to (or less than) the marginal costs of the step.

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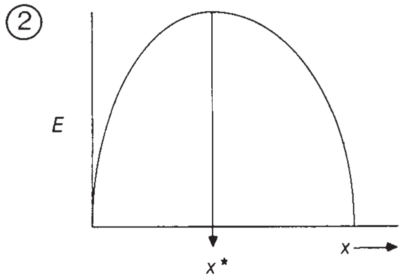

(3) A possible way in which the indirect criterion (energy gain E) might convert into direct fitness (number of progeny W). We assume that after some large number N of movements, the total energy gained, $E = NE(x)$, is converted into total babies produced following the relationship $W(E)$. We now ask the question whether the optimal strategy under the indirect criterion will be optimal under the true criterion (fitness). The true optimum is found by maximizing $W(NE(x))$, that is, by again setting

$$\frac{\delta W(NE(x))}{\delta x} = 0$$

subject to

$$\frac{\delta^2 W(NE(x))}{\delta x^2} < 0.$$

This gives the result that

$$N.W'(E)[B'(x) - C'(x)] = 0.$$

Because $N > 0$, then providing that W is always increasing in E (more energy means more babies), $W'(E) > 0$, so that as before $B'(x^*) = C'(x^*)$. The exact form of $W(E)$ is irrelevant, both the direct and indirect criteria give the same optimum, x^*.

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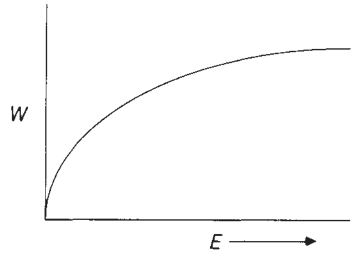

(4) Charnov's marginal value theorem[28] relates to an animal foraging amongst a series of patches that contain prey items. The cumulative calorific gain E through foraging for time t in a patch shows diminishing returns. Time s is spent each time the animal moves between patches. The optimization criterion is the overall rate of gain from the habitat, and the question concerns the optimal time, t^*, to spend in each patch. This is found by maximizing $E(t)/(s+t)$, which gives the result that

$$E'(t^*) = E(t^*)/(s + t^*)$$

which can be demonstrated graphically by drawing the tangent to $E(t)$ as shown.

Whether t^* is the true optimum depends on whether babies are produced at the end of a long time foraging (as Charnov's model intended), or whether they are produced at the end of each foraging bout, before the animal moves on to the next patch. If the animal has a fixed (long) time T available it will visit $T/(s+t)$ patches before it must finally convert its total gain G (where $G = E(t).T/(s+t)$) into babies W; the true optimum is therefore found by differentiating $W(G)$ with respect to t. The result is

$$T.W'(G)[E'(t^*) - E(t^*)/(s + t^*)] = 0.$$

This gives the same conclusion as in the lapwing model above; that is, provided that $W'(G) > 0$ (the more total energy gained the more babies are produced), t^* is the same for the direct and indirect criteria.

But this will not be so if babies are produced after foraging in each patch. In this case the total babies produced in time T is

$$W(E(t)).T/[s + t].$$

Differentiating this fitness function with respect to t now gives the result that

$$W'(E).E'(t^*) = W(E(t^*))/(s + t^*).$$

This is again a marginal value solution, but it stipulates that the tangent must be drawn to the direct fitness function, $W(E(t^*))$. It is easy to see that this is not equivalent to the marginal value solution for the indirect fitness function:

$$E'(t^*) = E(t^*)/(s + t^*)$$

unless the conversion between energy E and babies W is linear, that is, unless $W = aE(t)$ where a is a positive constant so that $W'(E) = a$. For this case then, the indirect criterion will result in an incorrect prediction of t^* unless it relates linearly to the direct criterion.

In general, it should be possible to investigate analytically whether—and under what conditions—an assumption of linearity will affect the predictions of a model.

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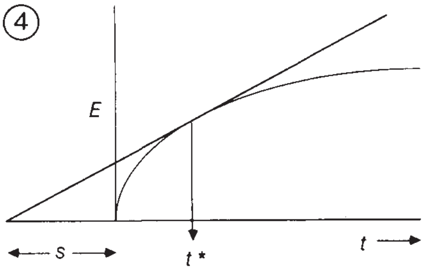


vary continuously if the strategy set is continuous, and can be termed 'fitness functions'. These usually depend on trade-offs between the counteracting costs and benefits of strategy changes. For example, in his sex-ratio theory, Fisher[10] assumed that all parents have equal resources to spend on the production of offspring, and that as a consequence, more sons would mean fewer daughters, and vice versa.

For specific models, fitness functions are often generated empirically, either experimentally, or by using the available natural variation, but both may pose serious problems[20]. As an illustration of the difficulties, consider the problem of optimal clutch size in birds. Lack[21,22] argued that the bigger the clutch, the more chicks that could be hatched. But the more chicks, the lower the chance that a given chick would survive, because the parents' input of food to the nest is limited. To build up a fitness function from natural variation, Lack recorded the initial clutch size in a nest (the variation defined the strategy set), and later counted the number of young fledgling (the fitness measure). The assumption here is that the natural variation is merely maladaptive noise. But this need not be so: parents with different resources might have different optimal clutch sizes. To overcome this problem, it is possible to alter experimentally the size of a series of clutches that were initially equal by adding or subtracting eggs as soon as egg-laying has finished, so as to measure directly the payoffs associated with different clutch-size strategies; but even this does not account for the costs to the parent of producing those eggs[20]. In reality, it is seldom certain that payoffs and fitness functions are true measures of the fitness of the strategies studied.

At least for general models, this is not a problem; payoffs must make sense qualitatively, but need not be defined precisely. Often, all that is required is that given relationships have a certain shape (for example, survival prospects of an offspring increase monotonically with the amount of parental care it receives[23]), or that relative payoffs are correctly ordered (for example, survival prospects of an offspring are higher when two parents care for it than when only one does[24]).

Once payoffs to the strategies have been stated, the optimal solution(s) are deduced by an appropriate analytical technique. This may involve no more than differentiating the fitness function and solving for the maximum (a simple example is worked through in Box 1). But there are a great many optimization techniques, many of them are borrowed from economics and engineering (see ref. 25). An important recent advance which allows analysis of optimal short-term, state-dependent decision-making is the application of stochastic dynamic programming in animal behaviour[7,26].

The final step in the optimality approach is to test the predictions, quantitatively or qualitatively, against the observations. If they fit, then the model may really reflect the forces that have moulded the adaptation. If they do not, we may have misidentified the strategy set, or the optimization criterion, or the payoffs; or the phenomenon we have chosen may not in fact any longer be adaptive. By reworking our assumptions, we modify our model and revise and retest the predictions. This has been criticized as being an iterative procedure leading inevitably to a fit. But this is how science works; theories can only be discarded when they are disproven or found to be unrealistic.

Two types of optimum

Optimization may be simple (frequency-independent) or competitive (frequency-dependent) depending on whether or not the optimum for an individual is affected by what other individuals do.

For an example of simple optimization consider the foraging behaviour of lapwings, which when searching for food typically move a few paces before pausing to look for their insect prey which are eaten if seen[27]. Over the observed range, the time spent stepping is trivial relative to pausing, but energy is expended at each step. Thus to deduce the optimal amount of movement between each bout of pausing, a plausible optimization criterion is the net gain of energy per bout.

If the distance moved is small, most of the ground will already have been inspected during the previous bout, making the discovery of a new food item unlikely. When the distance moved equals the diameter of the visual field, further movement does not help. The expected energy gain will show an asymptotic relationship with distance moved x, whereas energetic costs are assumed to rise linearly with x (Box 1.1). Net energy gains are found by subtracting costs from benefits (Box 1.2). Assuming that it pays to move at all, the optimal strategy (x^*) is the distance that maximizes energy gain; it can be calculated by differentiating the fitness function as shown in Box 1. This is a simple (frequency-independent) optimum because the best strategy depends only on the energetic costs of moving each unit of the diameter of the visual field, and not on the strategies of other lapwings.

If the indirect criterion is not, as assumed, linearly related to fitness (see Box 1.3), the predictions may or may not be reliable, depending on the nature of the model. In the above example, linearity is not essential, but Box 1.4 shows that one version of the marginal value theorem[13,28]—which predicts how long to stay in a food patch—does require the assumption of linearity, though Charnov's[28] original version does not.

By way of contrast, the optimal foraging rate of an individual in a flock of birds searching for berries in a tree is not simple, but depends on the behaviour of other individuals. Thus, whereas a solitary bird may consume berries at a slow rate because it has no competitors, in a flock, any bird that forages at a higher speed than the rest obtains a larger share of the berries. The best strategy now depends critically on the foraging rates of other birds, and payoffs now depend on the frequencies of strategies in the population. It is possible, under such circumstances, to seek a competitive equilibrium or evolutionarily

BOX 2 **Conditions for a strategy *I* to be an ESS against all alternative strategies *J* (refs 1, 2, 31)**

There are two conditions:

$$W(I, \mathrm{Pop}_I) \geqslant W(J, \mathrm{Pop}_I) \text{ for all } J \qquad (1)$$

where $W(I, \mathrm{Pop}_I)$ is the payoff to a single I strategist in a population of I strategists, and $W(J, \mathrm{Pop}_I)$ is the payoff to a rare mutant J strategist in the same population. For continuous fitness functions where the ESS is a unique competitive optimum, we can solve for the ESS after the method outlined in Box 2.

But suppose that

$$W(I, \mathrm{Pop}_I) = W(J, \mathrm{Pop}_I) \qquad (2a)$$

that is, some mutant strategy J can achieve a payoff equal to the payoff of I in a population of I. Then we require that

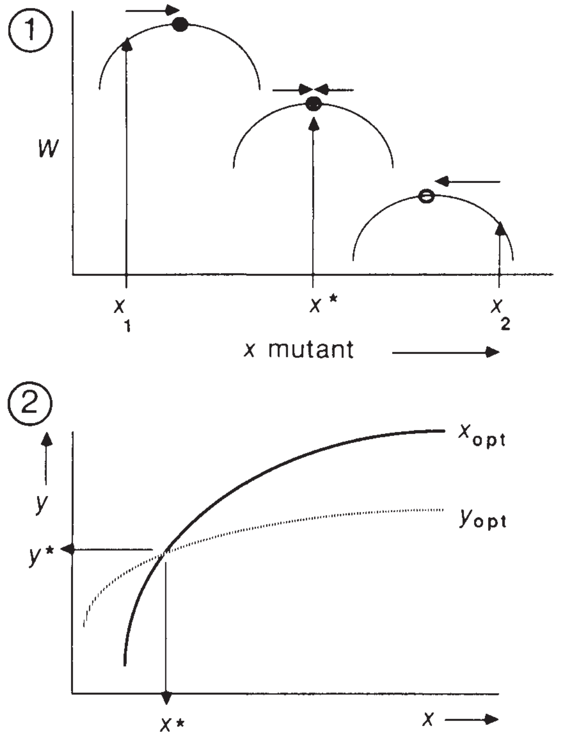
$$W(I, \mathrm{Pop}_{I,\Delta J}) > W(J, \mathrm{Pop}_{I,\Delta J}) \qquad (2b)$$

in which $\mathrm{Pop}_{I,\Delta J}$ is a population of I in which there is a sufficiently small proportion of J.

Condition 2*b* simply ensures that if J achieves an equal payoff when rare, it is lost by selection as soon as its frequency increases sufficiently by genetic drift. It has a special relevance when the ESS is a mixed strategy (for example, play strategy, S_1 with probability p_1, play strategy S_2 with probability p_2, ... et cetera, where $p_1, p_2, \ldots$ et cetera, are prescribed by the ESS). In this case, any one of the component pure strategies (for example, S_1 or S_2 et cetera) played with probability 1, or any rare alternative mixed strategy (in which the same pure strategies are played with different probabilities from the ESS) will obey equation 2*a*, because a condition for a mixed strategy to be an ESS is that each of the component strategies is equally rewarding when played in a population exhibiting the mixed ESS.

The study of ESS theory and its application to biological problems has expanded rapidly during the past decade or so, and owes much to the mathematics of game theory[2,29]. An ESS which obeys condition 1 is equivalent to the game-theoretical concept of a Nash equilibrium, though the ESS condition 2 has no parallel in game theory[19].

BOX 3 **An example of competitive optimization with continuous fitness functions**



(1) Fitness W achieved by mutants deviating continuously in strategy x, when the population is fixed at either x_1, or x^*, or x_2. In the bird flock example in the text, x is a foraging speed, and energetic costs of foraging increase wiith speed. But birds forage in flocks, and so individuals with higher than average foraging rates gain a higher than average proportion of the berries in each tree. It is assumed that the energetic costs of moving to another tree are high. A more explicit formulation of this type of model has been analysed by Parker[32]. In a population that plays strategy x_1, a bird that deviates by playing higher rates of foraging achieves a higher payoff, W. The best strategy in the x_1 population is shown by the circled dot. In a population where birds play the high foraging rate x_2, the reverse applies, deviations towards lower rates of foraging are favoured. Hence neither x_1 nor x_2 can be stable; selection will tend to favour values of x as indicated by the arrows. In the ESS population, x^*, any mutants deviating from the foraging rate x^* receive lower payoffs: x^* satisfies ESS condition 1. Following the notation in condition 1, we can solve for x^* by setting

$$\left.\frac{\delta W(x, \mathrm{Pop}_{x^*})}{\delta x}\right|_{x=x^*} = 0$$

subject to

$$\left.\frac{\delta^2 W(x, \mathrm{Pop}_{x^*})}{\delta x^2}\right|_{x=x^*}$$

This technique guarantees only local stability; it will be necessary to check that extreme mutants cannot invade.

(2) Games in which one continuous strategy set plays against another continuous strategy set. There are several biological games in which one strategy always plays against a different strategy. Examples include parent-offspring conflict, where the offspring strategy may be a begging level and the parental strategy may be a parental investment level[23], and sexual conflict, where the male strategy may be a courtship persistence level and the female strategy a courtship resistance level. Let the two opponents be X and Y, and let their continuous strategies be x and y. The graph shows the line of x_{opt}—the best strategies for X to play against all possible strategies played by Y, and the line of y_{opt}—the best replies of Y against X. The ESS is the pair of strategies x^*, y^*; these occur at the intersection of the two lines of best replies. In an x^*, y^* population, mutants deviating unilaterally in y or x will receive lower payoffs; the ESS will again satisfy condition 1. Following the same notation as in (1), we can solve for x^* by setting

$$\left.\frac{\delta W(x, \mathrm{Pop}_{x^*y^*})}{\delta x}\right|_{x=x^*} = 0$$

subject to

$$\left.\frac{\delta^2 W(x, \mathrm{Pop}_{x^*y^*})}{\delta x^2}\right|_{x=x^*} = 0.$$

Strategy y^* is solved in the parallel fashion (by interchanging x and y, and evaluating at $y=y^*$.

stable strategy (ESS) (ref. 2) using mathematical techniques derived from game theory[29]. The conditions for a strategy to be an ESS were first proposed by Maynard Smith and Price[29] and are outlined in Box 2.

The fitness function for ESS analysis prescribes the payoffs to rare mutants which deviate in strategy from the rest of the population. In our example of the bird flock, we anticipate that: (1) if the average foraging rate is low, a mutant that forages faster does better because it gets a bigger share of the berries; (2) if the average foraging rate is high, a mutant that forages slower does better because it spends less on foraging (see Box 3.1). In the ESS population, a mutant that forages at the average rate for the population does best; that is, the ESS is uninvadable by any alternative mutant strategy as defined in Box 2. In the example of the bird flock, each individual has equal strategic possibilities. But the same technique can be used to analyse games between different types of individual (for example, males and females; parents and offspring) who may play quite different strategies (see Box 3.2).

An ESS is not the strategy that maximizes fitness in a population sense (though this can be the case). In Box 3.1, maximum population fitness is achieved when the foraging speed is low, but such a strategy is not a competitive optimum or ESS, because it is invadable by a mutant that forages faster. In the ESS population, fitness is maximized only in the sense that mutants not playing the ESS do worse.

Many optimality models have globally stable equilibrium solutions towards which selection is expected to converge. Quite often, however, a given equilibrium is stable only locally (against mutants showing small deviations from it) and if an extreme mutation arises, or if the population contains high frequencies of alternative strategies, selection may drive towards a different equilibrium. Multiple equilibria are common in ESS models. Likewise, in simple optimization there may be several 'adaptive peaks' so that the outcome of selection depends critically on the starting conditions.

Can natural selection optimize?

The ability of natural selection to optimize depends on gene expression and on the mechanism of genetic change in populations. Of particular importance are the rate at which selection can alter the genetic structure, the amount of additive genetic variance present at the start of selection, gene flow (for example, that arising from immigration), the rate at which conditions change, and random effects such as genetic drift.

Most optimality models assume that strategies reproduce asexually, or if the model is mendelian, that the optimal phenotype can breed true. Pleiotropy (genes affecting multiple traits) is assumed not to operate and strategies are allowed to replicate independently of each other. Obviously, selection cannot produce an optimum if there is no way of achieving it genetically, but for some models, it is clear that selection will get as close to the optimum as the genetic mechanism will allow[33].

If selection can produce optima it is necessary to explain the natural variability found in populations. Such variation is viewed by some (the 'balancing-selectionist' school of ecological genetics) as being selectively maintained balanced polymorphisms, and by others (the 'neutralists') as being selectively neutral. Heterogeneity and changing conditions must mean that often populations are not perched at adaptive peaks. Even when conditions are constant, selection becomes progressively weaker towards the peak of a continuous fitness function; infinite time and infinite populations would be needed to achieve the peak itself.

Environmental effects will also generate variation, and this can be important in determining the optimal genotype[34]. For example, if a normal probability distribution of phenotypes arises from a given genotype and fitness as a function of phenotype is skewed, the optimal genotype will not correspond to the peak of the fitness function—it will lie on the side where the fall is less steep, where random deviation from the genotypic mean is less heavily penalized.

Competitive optimization poses special problems. Sometimes the predicted ESS is a mixed strategy consisting of a set of pure strategies played with probabilities prescribed by the ESS, posing various difficulties beyond our scope (but see ref. 2). Some game theoretical treatments (such as games in extensive form[35]) can become so complex that it is difficult to choose between large numbers of candidate ESSs. Some models do not generate any optimum or ESS, instead the strategy (or gene) frequencies change cyclically or chaotically without stabilizing. If these models are founded on the correct biological assumptions, then of course optimization cannot be expected. In certain instances, there can be a locally stable optimum or attractor, outside which there is cycling or bounded chaos. The outcome then depends on the starting conditions.

Difficulties

It is often difficult to decide the information constraints for the optimization; this relates to the fine-tuning of adaptation. Selection may merely generate an optimal response to the weighted mean of a wide set of conditions. If discrimination is possible, separate adaptive optima might be expected under different conditions. Yet finer tuning would allow graded responses to a continuous environmental variable (for example, a temperature cline) such that the response curve is optimal. The ultimate adaptive response could be some function of *n* variables, where *n* is a very large number. Only the most ardent pan-selectionist would suppose that there can be no limit to the complexity of the adaptive response surface. Perceptual limits alone must impose limits on ability to achieve perfection, and the information plausibly available to the animal will critically affect the predictions of a model.

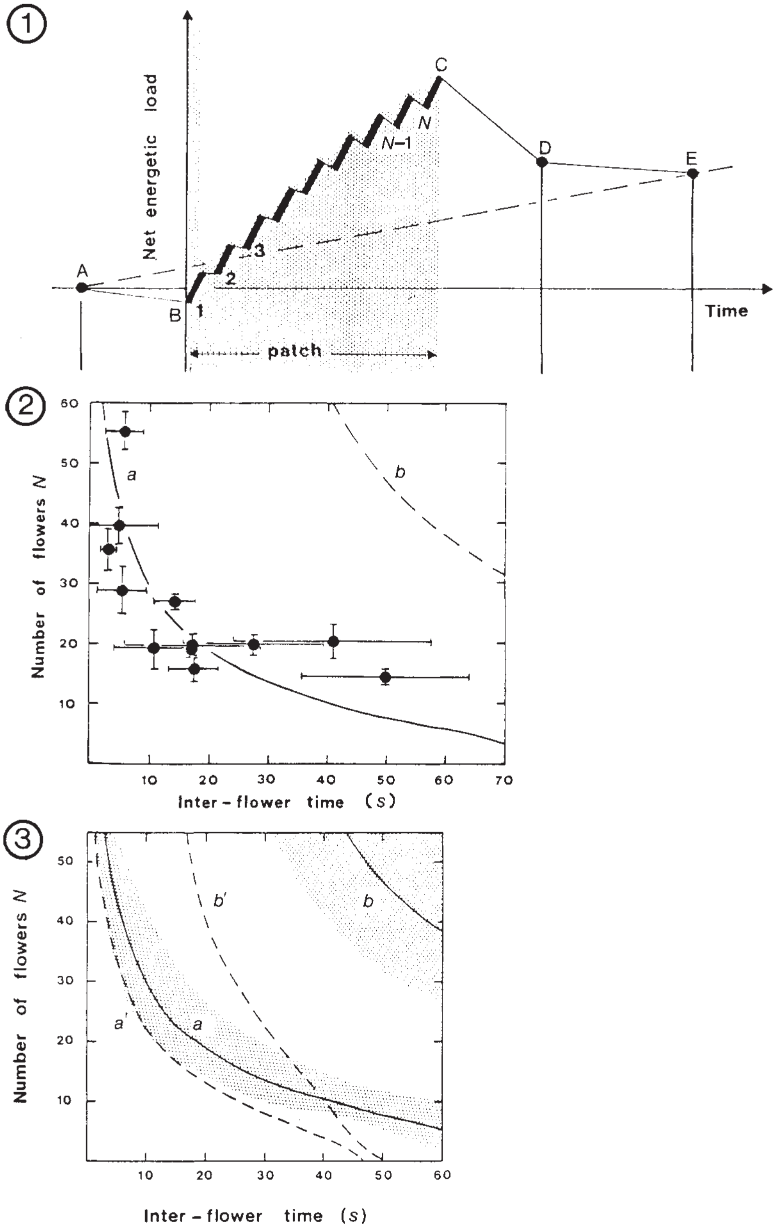
The fit demanded between the predictions of a model and observation depends on the nature of the model. The simple, 'general' type of model will contain very few assumptions, and can be expected to make only qualitatively correct predictions. But if these are sufficiently striking, the model has served its purpose. Two examples will illustrate this point. Hamilton[11] predicted that, if the offspring of a single female mate among themselves before dispersal (this is often the case, for example, in those parasitic hymenoptera in which a female lays many eggs in a single host), the sex ratio should be strongly female-biased. This prediction is born out. Hamilton went on to ask what is the optimal sex ratio if more than one female lays eggs in a single host. He got an answer that is qualitatively correct (the bias should be less extreme), but quantitatively inexact, because he did not allow for the fact that the second female is able to perceive that the host is already parasitized. To give a second example, we[36] predicted that a contest between the owner of a resource and an interloper should be settled conventionally in favour of the former, even if there is no difference in fighting ability or prospective payoff. This prediction has also been confirmed[37,38], but most real contests are complicated by secondary asymmetries, for example in size[39] or in the value of the resource[40].

In contrast, 'specific' models are intended to describe a single species in a particular environment, and therefore can give quantitatively accurate predictions. There are many examples where optimality models have generated predictions that match the observations; we just give one example as a case study. It is the work of Schmid-Hempel, Kacelnik and Houston[41] on honeybee foraging (Box 4). A worker bee visits flower patches repeatedly to gather nectar; between visits the nectar is returned to the hive. Assuming that the nectar available in the flower patch does not deplete (at least over the short term), then filling the crop at each visit would maximize the net rate of energy extraction from the food sources, which is commonly used as the optimization criterion in nectarivore foraging studies[42]. But bees often leave food sources when their crops are only partially filled[43], which cannot maximize the net rate of energy extraction. Models that include the metabolic costs of transport of nectar (during the patch visit and back to the hive) can predict that only part of the crop should be filled. The observed crop loads fit less well with those predicted when the optimization criterion is net energy gain per unit time than when it is net energy gain per unit energy expended (Box 4). The latter criterion would be more plausible if a worker bee's survival decreases with the amount of flight; that is, if it has a fixed energy budget for flight activity. Recent evidence suggests that foraging effort can reduce survival, though the effect is so far demonstrable only at excessive work loads[44,45]. This study shows how the optimality approach can be used to discriminate between various alternative hypotheses (in this case, alternative optimization criteria) so as to gain better insight into the nature of adaptation (in this case, partial crop loading by worker bees) under the biological constraints (the various metabolic costs of flight, and the costs of flight on body condition).

When discriminating between different models it is vital to test both their assumptions as well as their predictions; a common error is to ignore assumptions, particularly if these have not been made explicit. For quantitative models, there is a problem in assessing the significance of a fit. Because the optimality model serves as a null hypothesis, ideally it must be shown that there are no statistical grounds for rejecting it. This poses two problems. First, although it is generally easy to estimate the variance of the data, it is usually unsatisfactory to assume that the prediction has no variance. Quantitative predictions are usually calculated from measured parameters (which clearly should be independent of the observations to be tested), each of which has its own variance; hence there is the problem of estimating the combined variance of the prediction. It is often useful to perform some sort of sensitivity analysis (as in Box 4) to determine the effects that parameter variations have on the prediction. Second, most statistical techniques are designed to tell us when to reject null hypotheses, rather than when to claim that predictions and observations are likely to be the same.

When there are several models, then the one giving the best fit to the data can be decided by some appropriate statistic. If the predictions of two models are similar; it becomes difficult to differentiate between them. If the models are themselves rather similar, and qualitative predictions alone are required, then there is probably little need to differentiate because heuristic aims will be satisfied by both. But if radically different models generate the same predictions, no progress can be made until some way is established for differentiating between them.

BOX 4 **Schmid-Hempel, Kacelnik and Houston's[41] study of foraging in worker honeybees**



(1) The net energetic load carried by a worker bee as a function of time during the foraging cycle. The bee leaves the hive at A and encounters the first flower in the flower patch at B, having lost some energy due to the flight. It then visits a series of flowers; 1, 2, 3, . . . , N, and at each gathers a fixed amount of energy in the form of nectar (shaded zone). As the crop load increases, the drop in energy due to the flight between flowers increases. The bee leaves the patch at C, after gathering from N flowers. It returns to the hive at D, having lost considerable energy due to the increased metabolic costs of flight as load increases. Between D and E the worker remains in the hive. The authors were able to calculate the gross energetic gain (G), the total energetic expenditure or loss (L) and the total time (T) per foraging cycle, each as a function of the number of flower visits (N). The slope of the broken line AE gives the net rate at which energy is delivered to the hive; if the optimization criterion is net energy gain per unit time = $(G-L)/T$, the slope of AE is maximized. For the alternative model where the optimization criterion is energy gain per unit energy expended = $(G-L)/L$, the time axis would be replaced by an axis of energy expenditure. Under each model, an optimal number of flower visits (N^*)—and hence an optimal crop loading—can be predicted. This depends on the typical inter-flower time.

(2) The number of flowers visited (N) as a function of the inter-flower time. The predicted number of flowers that should be visited under the two models is shown by the two curves in the graph; broken curve (*b*) is for maximization of net energy gain per time, and solid curve (*a*) is for maximization of net energy gain per energy expended. In both models, N^* decreases with inter-flower time, and both models predict partial crop loads at high inter-flower times (a full crop is approximately 55 flower visits). The observations for 12 different individuals are shown (●, mean; bars, standard deviation). They clearly fit curve *a* better than curve *b*, and analysis showed that the observations differ significantly from *b*, but not from *a*.

(3) Sensitivity of the model predictions to changes in the parameter values. Curves *a* and *b* are the same as in 2 above. The shaded areas around these curves show the range of predictions obtained by halving or doubling in turn each of the four parameter values for the metabolic rate for the bees (unloaded rate; increment in rate due unit load increase, flower handling rate, and hive rate). In particular, the energy gain per energy expended model appears to be very robust, and insensitive to these changes in parameter values. The broken lines (*a'*; *b'*) are the predictions if the hive activity part of the foraging cycle (D to E in 1 above) is omitted from the models. This affects the quantitative conclusions but not the qualitative conclusion that the better fit is gained by the energy gain per energy expended model. The authors conclude that there are no *a priori* reasons for such an omission. Further support for this interpretation of honeybee foraging strategy has been obtained from recent physiological studies on metabolic rates[46], and the fact that altering the volume of sugar solution available per visit to artificial flowers gives changes in number of flower visits that again fit only the energy gain per energy expended model[47].

Alternative approaches

Two other methods have been used in analysing the role of selection in evolution: the comparative method, and quantitative genetics. The former goes back to Darwin. In its modern form[48], it consists of a statistical analysis of the ecological and phenotypic characteristics of a set of species. It can be carried out 'blind', in the hope that the pattern of observed correlations will suggest a selective explanation. Alternatively, it can be used to test some specific hypothesis. For example, Clutton-Brock *et al.*[49] used the comparative method to decide between two explanations for sexual dimorphism in size in primates: that it is a consequence of competition between males for females, or that it facilitates an ecological division of labour between the sexes. Because dimorphism is least in those species in which the breeding group is a monogamous pair, they conclude that male-male competition is the more likely explanation. The method has been extensively used to analyse behavioural, morphological and life-history evolution. It is a complement to rather than an alternative to optimization.

The approach from quantitative genetics[50,51] depends on the measurement of genetic variances and covariances. The response of a population to selection depends on the genetic variance, and if there is a genetic covariance between traits A and B, selection on A will change B. A criticism of this approach is that genetic covariances are hard to measure, and are unlikely to be a constant and stable feature of a species. But in some cases such covariances may reflect a fundamental physiological constraint. For example, Rose and Charlesworth[52] found a negative covariance between longevity and female fecundity in *Drosophila*. One reason for thinking that this may be a rather stable characteristic is that there is physiological evidence[53] that treatments (including 5,000 rads of X rays) that reduce egg-laying in *Drosophila* also prolong life. This example shows how the discovery of a genetic covariance can indicate the presence of a developmental constraint that must be taken into account in formulating an optimization model—in this case a model of life-history evolution. Most often, however, physiological experiments and interspecies comparisons may be easier ways of discovering such constraints.

To summarize on alternative approaches, quantitative genetics can help to identify the constraints needed for a satisfactory optimization model, and the comparative method is a powerful tool for testing the predictions of such models.

Future prospects

It is not surprising that optimality theory in evolution has antagonists as well as protagonists. Some of the critics of optimality theory—often theoretical geneticists—have tended to focus on the genetic problems of reaching optima. On the other hand, adaptationists such as behavioural ecologists have tended to proceed with faith in the power of selection, using optimization models as a tool to understand adaptation. We see both disciplines as perfectly worthy of study, and not contradictory. A start has been made in comparing the predictions of game theoretic and diploid genetic models[33], but further work is needed. A problem of particular interest from this point of view is that of the mate choice aspect of sexual selection. This would seem to be an ideal topic for analysis using game theory, because the optimal strategy for each sex depends on the behaviour of the other. So far, most analyses have involved explicit genetic models[54–56], but recently Grafen[57] has given a game theoretical analysis.

Similarly, in recent years students of animal behaviour have tended to belong to one of two schools. One group have sought the 'function' of behaviour and the selective forces responsible for its evolution. Others have had a primarily 'causal' or mechanistic interest, seeking to understand how the brain, together with sensory and motor organs, generates behaviour. Users of optimization theory belong to the first of these two schools, but they are forced to make assumptions about constraints: that is, assumptions about what is physiologically possible. Again, further progress is therefore likely to depend on collaboration rather than antagonism between the two schools.

In conclusion, optimization is one of the most powerful and elegant tools for understanding adaptation. None of its inherent problems call for its abandonment[58], though this has been advocated[59]. But we should be aware of the difficulties. ☐

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ACKNOWLEDGEMENTS. We are especially grateful to Steve Stearns, Alasdair Houston, Paul Schmid-Hempel, David Harper and Leigh Simmons for kindly commenting on various drafts of the manuscript.