# *Optimization and Adaptation*

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"A biologist who posited adaptation would be like a physicist who posited that bodies fall. Competent biologists treat the occurrence of adaptation or maladaptation as contingent in the same way that competent physicists treat the rising and falling of bodies as contingent. Adaptation has to be hypothesized and tested like everything else in science... . The new adaptational biology is neither Panglossian nor pluralistic, but tests broad, general hypotheses against hard data and is not satisfied until all contradictions have been purged from the system. This paradigm ... is Darwin's paradigm, revived and modernized." (Ghiselin, 1983)

## I. Summary

The optimization approach to the study of adaptation uses phenotypic models to ask which character states from a specified range of alternatives (the strategy set) are expected to be most fit or "optimal" under a suitable measure of fitness (the objective function), given other relevant assumptions about the biological situation being considered. To ask what is the best available character state, an investigator must confront the often critical issues of costs, benefits, constraints, and trade-offs that limit the possible or feasible phenotypic alternatives. Optimization models have been applied most often and most successfully to quantitative traits such as clutch sizes and sex ratios, where resource allocations subject to well-defined trade-offs have large effects on fitness. The productivity of the optimization approach derives from its requirement that the strategy set, the objective function, and other assumptions be clearly defined, and from its tendency to raise questions about the connections between different aspects of a species' biology. Optimization models assume that sufficient heritable variation will arise to permit the phenotypes under study to evolve toward their equilibria under the specified constraints, but this does not mean that they

necessarily ignore or deny historical contingency. Often there are constraints on the evolution of a trait that can be understood only as outcomes of the unique history of a lineage. The optimization approach to adaptation is not based on the assumption that organisms are "optimal" in any global or metaphysical sense, and in fact it often reveals that they are far less than "perfectly" adapted.

## II. Introduction

Living things give the appearance of having been designed for a purpose. Darwin's great discovery was that designs more intricate than any produced by human artifice can emerge from the mindless process of natural selection which simply compares heritable variants statistically with respect to their effects on reproduction. The selectively guided exploration of alternatives in the "neighborhood" of an existing design allows new variants with higher than average fitness to supplant older variants that were themselves fitter than those that they supplanted. A succession of such incremental substitutions can quickly improve a design, and eventually transform it radically (Dawkins, 1986; Dennett, 1995). Human engineers have come to appreciate the power of this process, which they use in the form of "genetic algorithms," to solve complex and otherwise difficult maximization problems (Holland, 1992, 1995; see also Chapter 14). In engineering, as in evolution, the fittest attainable solution is often a compromise, owing to *constraints* on the feasible design options and *trade-offs* among different benefits to be achieved by the design. The selective accumulation of variants that confer increased fitness therefore tends to *optimize* the parameters of the design with respect to the organism's (or engineered system's) overall state of local adaptation.

Optimization is about constraints and trade-offs, not "perfection." The fittest conceivable organism would live forever, reproducing continually at an infinite rate. The fittest possible organisms do far worse than this because they are constrained either absolutely or effectively by laws of physics, by deeply rooted evolutionary legacies, and by complex trade-offs among individually attainable but mutually incompatible character states. For example, two beneficial activities such as eating and watching for predators may be incompatible simply because they cannot be pursued at the same time. In a famous passage from the *Origin*, Darwin (1859) asks us to appreciate that "natural selection is daily and hourly scrutinizing, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life." This passage vividly evokes the relentlessness of selection but only hints that the difference between "bad" and "good" designs may often hinge on trade-offs.

Some trade-offs take similar forms wherever they arise, even though the fittest compromise may vary with aspects of the species' biology and environment. For example, parents usually face a trade-off between the number of offspring they can produce and the sizes of individual offspring, because

their total reproductive effort is limited (Smith and Fretwell, 1974; Charnov and Downhower, 1995; Charnov et al., 1995). Other trade-offs derive as much from a species' history as from its current ecology. Selection chooses only among current alternatives, with no foresight, so adaptive pathways taken at one time may cast very long shadows into the future of a lineage, affecting what "opportunity offers" (Darwin's subtle acknowledgment of contingency in the quote above) at any given time. For example, the basic skeletal organization of amphibians, reptiles, birds, and mammals poses countless optimization problems today that owe their forms in large part to ancient adaptations for swimming like a fish. But whether relatively universal and recurring or relatively particular and historically conditioned, constraints that establish trade-offs set the stage for a diversity of solutions that may evolve through locally optimizing exploration of the set of accessible character-state combinations. Ecological specialization and evolutionary diversification may therefore be driven in large part by trade-offs that force species to choose, in effect, among restricted combinations of character states that will be simultaneously both compatible and competitive (e.g., Joshi and Thompson, 1995).

Biologists seeking to understand how the designed features of organisms were assembled, how they reflect underlying constraints, and how well they serve their functions are engaged in what amounts to a grand reverse-engineering project (see Dennett, 1995). Since the engineering was accomplished by cumulative selection rather than by conscious planning and experiment, biologists may have little choice but to begin by asking how the features under study might have been optimized for one or more functions, under one or more constraints. In a general sense, then, optimization is a fundamental principle of evolutionary biology, especially of the study of adaptation. However, to say that optimization permeates almost every problem in biology is not to say that it answers every question, nor is it to say that characters (even ones with strong effects on fitness) are necessarily expected to be found in optimal states.

This distinction between the *process* of optimization and the *state* of optimality is important. The process is ubiquitous and powerful, but the state can be elusive. In an unchanging environment, with an adequate supply of variation, most characters that affected fitness would be at least locally optimal in the sense that for all practical purposes selection acting in the here-and-now could not improve them given the prevailing constraints on the joint ranges of attainable character states (Charnov, 1989; Charlesworth, 1990). A species' phenotype would then tell us a great deal about its environment because there would be a direct mapping (mediated by genotypes) between its selective regime and its phenotype. But of course the world is nowhere near this simple. Environments may change, deleterious mutations may accumulate, and the ranges of accessible character states may be limited in complex, seemingly arbitrary ways that have more to do with a species' history, genetics, and developmental biology than with the demands and opportunities created by its way of life. Thus in the real world, the state of near-perfect adaptation, optimality, could be relatively rare, while the process of optimization is improving phenotypes everywhere and at all times (subject to prevailing constraints), by changing gene frequencies in ways that increase fitness.

The optimization approach to the study of adaptation can be very

productive even where the attainment of optimality cannot be assumed. Indeed, optimization models often yield valuable insights when they fail by raising previously unasked questions about connections among particular aspects of the biologies of the species under study. This happens because optimization models focus attention on processes that give rise to selection pressures and on constraints that modulate a population's evolutionary responses to selection. The specific questions and hypotheses that emerge often motivate empirical tests that advance our understanding of the ways in which adaptive designs both evolve and fail to evolve.

In what follows we first outline the structure of an idealized optimization study, emphasizing the differences between the model itself, its analysis, and its tests. Next we review the origins of the optimization approach, comment on its aims and limits, and critically examine the elements of the model: the actors, currencies, objective functions, strategy sets, and constraints of many kinds. We conclude with some thoughts about the future evolution of the approach, including its possible application to emerging problems in genetics and development.

Various aspects of this subject have been reviewed, from different perspectives, by many authors including Williams (1966a, 1992), Levins (1966, 1968), Leigh (1971), Schoener (1971), Cody (1974), Pyke et al. (1977), Rapport and Turner (1977), Lewontin (1978, 1979, 1984), Maynard Smith (1978), Oster and Wilson (1978), Gould and Lewontin (1979), Horn (1979), Beatty (1980), Alexander (1982), Charnov (1982, 1993), Mayr (1983), Emlen (1984), Maynard Smith et al. (1985), Stephens and Krebs (1986), various authors in Dupré (1987), Mitchell and Valone (1990), Parker and Maynard Smith (1990), Thornhill (1990), Grafen (1991), Lessells (1991), Sibly and Antonovics (1992), Stearns (1992), Moore and Boake (1994), Orzack and Sober (1994a,b), Roff (1994), Bulmer (1994), Dennett (1995), and others. We have absorbed many ideas from these works, both consciously and unconsciously. The papers and books we cite in this chapter provide useful starting points for readers who want to explore on their own, but they inevitably reflect our personal interests, biases, and limited mastery of the huge literature on this complex subject. We apologize for the slights we will inevitably commit, unintentionally, to authors both cited and uncited.

## III. The Structure of an Optimization Study

An optimization study is motivated by questions derived from some perceived problem concerning the form or taxonomic distribution of a possible adaptation. The study itself consists of three main parts: (1) a *model* that embodies explicit assumptions about the biological situation under study, casting it in a simplified, abstract form and defining the quantity that selection is expected to optimize; (2) an *analysis* that deduces the optimum, which may vary as a function of the model's parameters; and (3) a *test* that asks how well the model's assumptions and the predicted optimum agree with relevant empirical data. As in other applications of the hypothetico-deductive method in science, this process may cycle repeatedly back to the beginning, with modified forms of the model being reanalyzed and retested in a search for sets of

assumptions that "work" in the sense that they "explain" the biological patterns that motivated the study (and others uncovered during the study) in a consistent and otherwise plausible way.

The model contains a number of distinct elements. First, it identifies the *actor*, typically an individual such as a foraging bird or a growing plant that expresses the phenotype(s) whose adaptive evolution we seek to understand. Sometimes the actor is a less inclusive entity such as a gene, and in principle it could be a more inclusive entity such as a local population. In any case, defining the actor establishes the scope of the model and the assumed locus of control (metaphorically, the point of view or interest) with respect to which the optimization is to occur.

Second, the model identifies a *currency* in which the fitnesses of alternative phenotypes can be evaluated, the *control variable(s)* that quantify the states of those phenotypes, and an *objective function* that describes how fitness (in units of the currency) depends on the control variable(s) and other aspects of the biological situation. For example, if the currency were "number of offspring reared to weaning" and the control variable were "number of zygotes conceived," then the objective function would give the number reared to weaning for each possible number of zygotes conceived.

Third, the model specifies a *strategy set* that describes the actor's options for manipulating the control variables. There is often much more to the strategy set than just a range of accessible values of the control variables. For example, the strategy set may allow the control variables to depend on states of the physical or social environment, or on the actor's individual circumstances such as age or size. Trade-offs and constraints of various kinds may appear either in the objective function or in the strategy set, depending on their origin. For example, a trade-off between the number of zygotes conceived and their probabilities of surviving to the age of weaning might naturally be built into the objective function, and the strategy set might then consist of all zygote numbers from zero to infinity. Or in a sex-ratio problem, the parent's fecundity might be fixed by random factors that vary among individuals, and the strategy set might include all sex ratios (proportions of male offspring, $r$) between 0 and 1, to be determined after the parent knows its own fecundity and possibly the fecundities of other individuals in its immediate neighborhood (e.g., Stubblefield and Seger, 1990).

These three kinds of assumptions define the model. When they have been fully specified the model can be analyzed to reveal which of the accessible strategies for manipulating the control variables gives the largest value of the objective function. Many different mathematical techniques are used to perform such analyses, depending on the structure of the model. In the simplest cases the objective function can be maximized by setting its derivatives with respect to the control variables equal to zero and solving the resulting system of equations. If the phenotype involves a temporal sequence of decisions, with early decisions affecting the consequences of later decisions (as in models of growth and reproduction), then dynamic programming techniques may be required. Where the fitness of a given phenotype depends on the distribution of other phenotypes in the population (as in sex-ratio problems), various kinds of stability analyses are used to find the "unbeatable" phenotype or distribution of phenotypes. Some models are so complex that

general closed-form solutions giving the optimal phenotype as a function of the model's parameters cannot be found. In such cases numerical methods are typically used to find particular solutions for given sets of parameters.

The results of an analysis may be of interest in their own right, since they describe inevitable consequences of the assumptions and these may have been unknown or unappreciated. In this sense all correctly analyzed models are "true" (as theory), whether they explain anything about the real world or not (Parker and Maynard Smith, 1990). But as always, a model becomes more interesting scientifically to the extent that its assumptions are plausible and its predictions unexpected. Interesting models therefore invite tests that evaluate their relevance to our understanding of the evolution of the (real) phenotypes in question.

These points are illustrated concretely by the following highly simplified account of work on the problem of clutch-size variation in birds. David Lack (1947, 1948, 1954) asked why there should be so much variation both among and within bird species in the numbers of eggs that parents lay and attempt to rear in a single bout of reproduction. Species produce average clutches ranging from one egg to more than a dozen, and even within a single species many parents may produce clutches far above and below the mean. Lack reasoned that selection should adapt the egg-laying behavior of parent birds to produce, at least on average, clutch sizes close to those that yield the largest number of surviving, reproductively successful offspring. Clutch sizes too small would yield fewer surviving offspring than the parents might have produced, and clutch sizes too large might also yield fewer than the maximum number of surviving offspring, perhaps by overtaxing the parents' ability to feed the nestlings prior to fledging. This might cause early mortality or low fledging weights that would impair the young birds' expectations of subsequent survival or successful reproduction as adults.

Lack's hypothesis defines a model in which the actors are parent birds, the currency is offspring number, the control variable is number of eggs laid, and the objective function gives the number of offspring surviving to reproduce as a function of the number of eggs laid. The most obvious constraint is the limited amount of food that parents can bring back to the nest during the period of nestling development. This constraint gives rise to a trade-off between the number of offspring reared and the average amount of food that each one can receive, and thereby to a well-defined relationship, in units of the currency, between the number of offspring reared and the probability that any one will survive to breed successfully as an adult. The model can therefore be formalized as $W = n \cdot P(n)$, where $W$ is parental fitness, $n$ is clutch size, and $P(n)$ is the probability that an egg will give rise to a reproductive adult offspring, as a function of $n$.

The analysis reveals that if $P(n)$ declines rapidly enough at larger values of $n$, then $W$ will have a "humped" or "domed" shape and there will be an optimal value of $n$ (denoted $n^*$) that maximizes parental fitness under the trade-offs embodied in $P(n)$. For example, if we suppose for purposes of illustration that $P(n) = 1 - an$, then it is easy to show by elementary calculus that $n^* = 1/2a$ (Fig. 1). This almost absurdly simple model makes an interesting and potentially testable qualitative prediction: in species or populations where the increase in offspring mortality with increasing clutch size is relatively fast, average clutches
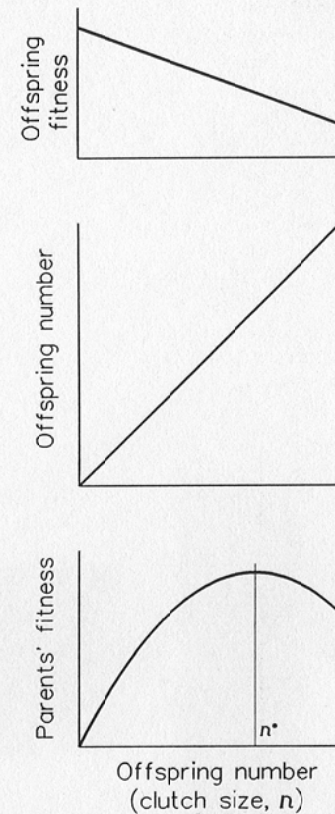


**Figure 1** Lack's model of clutch-size regulation. The fitness of each individual offspring is assumed to decline as clutch size increases, due mainly to limits on the parents' ability to feed nestlings. The parents' fitness (bottom) can therefore be expressed as a product of the average offspring fitness (top) and the number of offspring produced (middle). This function has a well-defined intermediate maximum (giving the optimal clutch size, $n^*$) for many plausible forms of the offspring fitness function (for example, where individual fitness declines monotonically and relatively more quickly at larger clutch sizes, as in the simple linear case shown here).

should be relatively small; where it is slow, they should be large. And of course within a population most parents should produce the "Lack clutch," which is the clutch that maximizes the number of offspring recruited (subsequently) into the adult breeding population.

This and many more elaborate versions of Lack's hypothesis have been tested over the last 40 years in many species of birds, perhaps most extensively in a population of great tits (*Parus major*, a close relative of North American chickadees) that nests in Wytham Wood near Oxford, England. A frequency distribution of clutch sizes for nearly 4500 clutches (distributed over 23 years) is

shown in Fig. 2, with the mean number of recruits produced by each clutch size from 4 to 14 (Boyce and Perrins, 1987). The most productive clutch is 12, but the commonest clutches are 8 and 9. Parents therefore appear to lay smaller clutches, on average, than those that would maximize their fitness. Similar patterns have also been found in other species. Thus Lack's hypothesis does not seem to be supported, at least not in this simple form and with this simple analysis of the data.

As the existence of systematic discrepancies between the Lack clutch and the most common clutch became evident, it was realized that parents should be selected to maximize their lifetime production of recruits, and that doing so might not involve maximizing their production in any one year (e.g., Williams, 1966b; Charnov and Krebs, 1974). If the effort involved in rearing a large brood this year so exhausts a parent that it is less likely to survive to breed again next year, or less able to feed a large brood next year, then there will be a between-years trade-off, and the clutch size that maximizes lifetime fitness may be smaller than the one that maximizes fitness in any one year. Such trade-offs have been found in several species (e.g., Gustafsson and Pärt, 1990; see Lessells, 1991; Roff, 1992; Sibly and Antonovics, 1992; Stearns, 1992), but not in the Wytham Wood population of great tits. A number of other modifications of the hypothesis have been suggested (reviewed by Boyce and Perrins, 1987 and the preceeding references) and several may provide part of the explanation.

The most important additional factor for great tits in Wytham Wood seems to be that parents respond adaptively to their own highly variable individual circumstances. Those that find themselves able to rear larger than average broods (for reasons of health, territory quality, early pair formation, and the like) lay larger than average clutches, while those that find themselves in
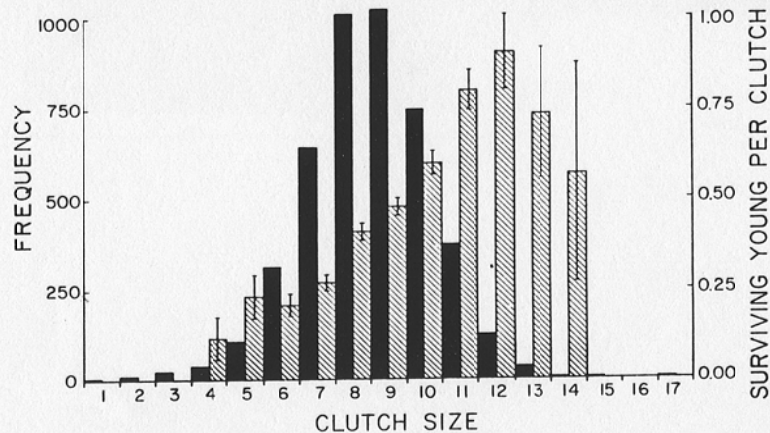


**Figure 2**  Clutch-size distribution and clutch-size-specific recruitment rates for great tits (*Parus major*) in Wytham Wood, 1960–1982. Solid bars show numbers of clutches of sizes from 1 to 17 eggs (*N*=4489). Hatched bars show mean numbers of young per clutch that survived to at least 1 year of age (±1 s.e.). From Boyce and Perrins (1987) courtesy of the authors and *Ecology*.
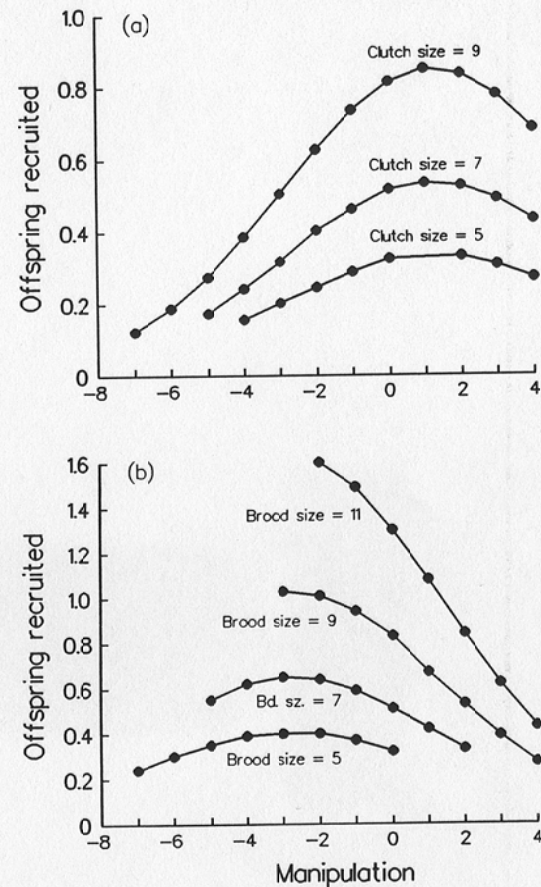


**Figure 3**  Offspring recruitment as a function of clutch-size manipulations for great tits in Wytham Wood. In both panels, the average number of offspring surviving to 1 year of age is estimated from a log linear model. (a) Numbers recruited are shown for *initial* clutch sizes of 5, 7, and 9 eggs. Thus the upper right-hand point represents clutches of 9 that were augmented by 4 newly hatched chicks, to a total (barring natural mortality) of 13. (b) Here the number recruited is shown for *final brood sizes* of 5, 7, 9, and 11 chicks. Thus the upper point represents a clutch of 13 eggs that was reduced by 2 to a final size of 11. Redrawn from Pettifor, Perrins and McCleery (1988) courtesy of the authors and *Nature*.

relatively poor condition lay smaller clutches. Thus the aggregate distribution shown in Fig. 2 is composed of many individual distributions for birds of different overall condition who have different Lack clutch sizes. How was this shown? Various hypotheses (including this one) had suggested that it would be interesting to know the success rates of broods from clutches that had been

experimentally enlarged or reduced in size. Newly hatched chicks were therefore transferred between nests in Wytham Wood for many years. The resulting data most strongly support the individual-optimization hypothesis (Pettifor et al., 1988) (see Fig. 3). It appears, then, that parents can assess their condition and adjust their attempted brood size to their actual brood-rearing ability in a given year.

This conclusion does not rest simply on the fact that the clutch-size manipulations support a prediction of the individual-optimization hypothesis. Many other kinds of data contribute to the overall support for this interpretation of great tit clutch sizes in Wytham Wood and to related hypotheses (often different in detail) for other populations and other species. Such data support the models by confirming their key assumptions. For example, data on fledgling weight as a function of clutch size and clutch manipulation show that parents are at or near the limits of their foraging abilities during nestling development and that the growth of nestlings is limited by food. Data on survival and subsequent reproductive success as functions of fledgling weight show that an offspring's prospects are indeed related to the food it received from its parents (see Lindén and Møller, 1989; Newton, 1989; Godfray et al., 1991; Lessells, 1991). In general, then, our confidence in models of clutch-size evolution derives as much or more from tests of their assumptions as it does from tests of their predictions about the clutch-size distributions themselves.

The study of clutch size in birds was thoroughly quantitative from the beginning and it has become very sophisticated (e.g., Daan et al., 1990). Its style of analysis has been applied to an ever wider range of taxa, including plants and invertebrates (see Godfray et al., 1991; Lessells, 1991), and it has served as a model for studies of other allocation problems. With this classic example as background, we will briefly consider the origins of the optimization approach, and its aims and domain of application, before taking a closer look at the key elements of a typical optimization model.

## IV. The Roots and Branches of Optimization

Evolution is a dynamical process without a goal or even a definite stopping point. Whether viewed at the level of phenotypes or of underlying genotypes, evolutionary trajectories just keep going and going as long as the population survives. This elementary but very important fact is appreciated better today than ever, due to many kinds of recent advances, including long-term studies of selection in nature (see Endler, 1986; Grant, 1986; Grant and Grant, 1989, 1993), a heightened concern with biotic (hence evolutionarily reactive) components of the environment (see Crawley, 1992; Thompson, 1994), and a rapidly accumulating wealth of molecular genetic data (see Gillespie, 1991).

In contrast, optima are fixed points that make no necessary reference to time or history; if you are there, you are there, no matter how you arrived. Looked at this way, optima seem counter-evolutionary, but they are connected to evolutionary trajectories in a way first made clear by Fisher's (1930) "Fundamental Theorem of Natural Selection", which shows that under suitable simplifying assumptions, gene frequencies will change so as to carry a

population along the path that tends to maximize the current rate at which mean fitness increases. The Theorem embodies a seductive and influential view of evolution in which selection appears as a tireless hill-climbing algorithm that inexorably moves a population along the line of locally steepest ascent on the "fitness surface" that defines the current "adaptive landscape" (Wright, 1931). In this population-genetic formulation, Darwin's relentless scrutinizer of variations becomes a blind but efficient optimizing daemon. If there is a peak in the fitness surface (a point from which fitness declines in all directions), then a nearby population will be attracted to it. Once on top, the population will remain there until the landscape deforms (i.e., the environment changes) in a way that creates an ascending route of egress.

This beautiful if oversimple vision of evolution implicitly identifies optima as the phenotypes associated with fitness maxima, under a model of the relationship between genotypes and phenotypes in which the genetic variation needed to produce the fitness-maximizing phenotypes is readily available to the population. Under the assumptions of this model, a population will move remarkably quickly to the vicinity of a locally attracting fitness maximum if the path of ascent is even moderately steep (which is to say, if selection on the character states in question is at all strong). A very important implication is that, on average, populations should be close to fitness peaks with respect to traits that strongly affect fitness, to the extent that the assumptions of the model are met. The two most important of these assumptions are, again, that the fitness landscape has not recently changed too dramatically and that genetic variation for the traits in question is adequate to allow them to evolve toward the optima. We will examine these critical assumptions below; here we note that for certain kinds of situations they can be defended both theoretically and empirically.

Darwin and Fisher understood clearly that selection tends to increase individual fitness, not group or species fitness. But the Fundamental Theorem does not embody this distinction because it assumes that the fitness associated with a given phenotype is independent of its frequency in the local population. Thus under the assumptions of the Theorem, an optimum phenotype can be found by maximizing the population's mean fitness. This procedure is harmless under the assumptions of the Theorem, but not where fitnesses are frequency dependent. During the first half of the 20th century many biologists began speaking of selection as a force that "acts for the good of the species." This largely unconscious retreat from individual selection culminated in 1962 with the publication of V.C. Wynne-Edwards' *Animal Dispersion in Relation to Social Behaviour*, which explicitly interprets mating aggregations as population-assessment mechanisms that enable individuals to adjust their reproduction downward at times of high population density so as to prevent their species from outstripping its resources. Such behavior might be "optimal" from the point of view of the species, but it would not maximize individual reproductive success (the criterion identified by Darwin with natural selection), and in fact it could evolve only under extreme assumptions.

Wynne-Edwards' book was criticized, most notably by Lack (1966) and by G.C. Williams, whose *Adaptation and Natural Selection* (1966a) demolished naive group-selectionist explanation in biology and restored natural selection as the principal agent of adaptive evolution. Williams argued that although selection is

an awesomely powerful process, adaptation remains an "onerous concept" to be invoked only for good reason. It is impossible to overstate the importance of this intellectual housecleaning. By bringing rigor to the analysis of adaptation and by establishing imperfection and conflict as ever present possibilities, *Adaptation and Natural Selection* set the stage for a flowering of optimization studies that could not possibly have occurred within the earlier non-Darwinian species-advantage framework.

Although the optimization approach as currently understood and practiced dates only from the middle 1960s, it has roots going back at least to Darwin, who appreciated not only the power of selection but also (if only at an impressionistic level) the possible importance of the kinds of constraints that now figure prominently in studies of allocation problems. For example, in his discussion of the evolution of plant sexual systems, Darwin (1877, pp. 280-281) invokes "the law of compensation" in an astonishingly modern hypothesis about how dioecy could evolve in an originally hermaphroditic species: A few individuals begin making seeds that are larger than average, and this is "highly beneficial" in the current environment; "but in accordance with the law of compensation we might expect that the individuals which produced such seeds would, if living under severe conditions, tend to produce less and less pollen, so that their anthers would be reduced in size and might ultimately become rudimentary"; then as the large-seeded proto-females became common, other individuals would "produce a larger supply of pollen, and such increased development would tend to reduce the female organs through the law of compensation, so as ultimately to leave them in a rudimentary condition; and the species would then become dioecious."

Many problems now studied within optimization frameworks have similarly deep roots. For example, Fisher saw how life history evolution could involve resource-based trade-offs between growth and reproduction: "There is something like a relic of creationist philosophy in arguing from the observation, let us say, that a cod spawns a million eggs, that therefore its offspring are subject to Natural Selection; and it has the disadvantage of excluding fecundity from the class of characteristics of which we may attempt to appreciate the aptitude. It would be instructive to know not only by what physiological mechanism a just apportionment is made between the nutriment devoted to the gonads and that devoted to the rest of the parental organism, but also what circumstances in the life-history and environment would render profitable the diversion of a greater or lesser share of the available resources toward reproduction" (Fisher, 1930, 1958, p. 47).

Fisher also explained why 1:1 sex ratios should be common in a brilliant but cryptic first application of the kind of analysis that would later become evolutionary game theory (1930, 1958, pp. 158-160). Darwin (1871, p. 399) was famously baffled by sex-ratio evolution, even though he seems to have come very close to grasping how sex allocation gives rise to frequency-dependent fitness payoffs, as suggested by the dynamics in his scenario for the evolution of dioecy (quoted above).

Darwin (1871) both framed the problem of sex differences and outlined the theory of sexual selection. Fisher (1915, 1930) greatly admired this work and extended it in ways that would later prove important. Otherwise, there were few significant contributions to sexual selection until the 1960s, aside from

some pioneering empirical work on mate choice in *Drosophila* by Bateman (1948) and others (reviewed by Andersson, 1993, pp. 17-19). Discussions of sexual selection seldom employ the language of optimization, even though the subject abounds with trade-offs involving aggression, advertisement, and mate choice, on the one hand, *versus* survival and offspring production, on the other. There are many possible reasons for this, including that secondary sex characters are obviously not "optimal" from a species-benefit point of view and that the dynamics of many kinds of sexual selection have long been understood to be inherently frequency dependent and therefore logically treated in explicitly game-theoretic kinds of frameworks.

Darwin, Fisher, and Haldane also anticipated, in different ways, the outlines of what is now known as inclusive-fitness theory or kin selection (Hamilton, 1964), another major branch of the optimization approach that emerged in the 1960s and grew explosively thereafter. Here the trade-off to be optimized, as a function of ecological (including social) circumstances, is one between direct reproduction and indirect or vicarious reproduction *via* relatives.

Why did these problems and ideas that exemplify the optimization approach remain nearly dormant for most of a century, and then burst into luxuriant growth at very nearly the same time? This fascinating question clearly needs more attention from historians of science, but some elements of the answer seem fairly obvious. We have mentioned the implicit group-selectionist outlook that would have forestalled the analysis of situations involving conflicts of interest. More generally, this outlook may have deflected attention away from factors associated with variation in lifetime individual reproductive success (see Clutton-Brock, 1988; Newton, 1989). It may be relevant that the pioneers of evolutionary theory in the first half of the 20th century (geneticists, naturalists, paleontologists, and systematists alike) were preoccupied with questions about elementary mechanical aspects of evolution, in an environment where the field's status was nowhere near as secure as it is today. Until this work was largely finished, many of the kinds of questions addressed today through optimization approaches might have seemed of secondary importance to those who happened to think about them.

Writing in the very early 1960s, Orians (1962) argued that ecology had been for many years an almost defiantly nonevolutionary discipline concerned mainly with mechanisms of population regulation, but that the separation between ecology and evolutionary biology was at last breaking down. Orians' paper is called "Natural Selection and Ecological Theory," and its main purpose is to celebrate the marriage that would give birth to evolutionary ecology, including the movement in community ecology associated with G.E. Hutchinson and R.H. MacArthur. Orians is explicit about the need to explain diversity rather than merely taking it as a given parameter of some other problem. The concepts of the niche and of limiting similarity were applied, in the first instance, to closely related, ecologically similar species that differed mainly in quantitative aspects of their phenotypes, such as sizes, or times and places of foraging. Thus the evolutionary changes at issue posed no mechanistic difficulties because they consisted almost entirely of simple adjustments to the means and variances of some ordinary quantitative characters that varied in similar ways within each of the species in question. We

would guess that this fusion of ecology and evolution was as important to the development of the optimization approach as was the exorcism of naive group selection. It encouraged both ecologists and evolutionists to think seriously about the causes and consequences of variation in the structural, behavioral, and reproductive parameters of sets of related species in their real ecological settings and it forced them to attempt to explain the evolution of those parameters primarily in terms of ecological opportunities and constraints.

In his approach to the problem of clutch-size variation in birds, Lack (1947, 1948, 1954, 1966) was far out in front of the trends discerned by Orians. The clutch-size problem was one of the first applications of the optimization approach to give rise to well integrated bodies of theory and data. It now defines a field of considerable size and sophistication, with well developed links to a range of general problems in foraging, life-history evolution, and even developmental biology (e.g., Newton, 1989; Daan et al., 1990; Gustaffson and Pärt, 1990; Meijer et al., 1990; Dhondt et al., 1991).

The modern evolutionary theory of senescence has roots going back to another early and remarkably advanced application of optimization thinking (Medawar, 1946, 1952; Williams, 1957; Hamilton, 1966; Charlesworth, 1980, 1994; reviewed by Rose, 1991; Partridge and Barton, 1993; see Chapter 7). This example is important for many reasons, including that the phenomenon to be explained (aging) appears at first to reflect a failure of adaptation. On closer examination this turns out to be only half true since there may be phenotypes that increase fitness early in life at the expense of fitness later in life, and *vice versa*: "A gene or combination of genes that [favors early reproduction at the expense of later reproduction] will under certain numerically definable conditions spread through a population simply because the younger animals it favours have, as a group, a relatively large contribution to make to the ancestry of the future population" (Medawar, 1946). Thus a shortened lifespan may evolve, in principle, by optimizing selection in the face of age-related trade-offs (see Bell and Koufopanou, 1986; Kirkwood and Rose, 1991).

Clutch sizes and patterns of senescence are specific elements of *life histories*, which can be defined as age-specific schedules of growth, reproduction, and mortality. Attempts to derive general theories of life-history evolution that could make sense of the great diversity of life histories seen within many groups of plants and animals have proceeded from the idea that schedules of growth, reproduction, and mortality should reflect evolutionary compromises among competing demands, under constraints that limit the possible combinations of vital rates (Gadgil and Bossert, 1970; Schaffer, 1974; Stearns, 1976). The models have become increasingly sophisticated and there has been much effort devoted to identifying, in comparative data, general patterns that can be used to test and refine the models (Lessells, 1991; Roff, 1992; Sibly and Antonovics, 1992; Stearns, 1992; Charnov, 1993).

The study of animal behavior has been transformed in recent decades by "strategic" analyses that extend and generalize the optimization approach. We have already mentioned sexual selection and kin selection, which gave rise to vigorous fields of theoretical and empirical research on mate choice and altruism. Many kinds of social behavior have adaptive landscapes that cannot be visualized and analyzed in the usual way because they are inherently frequency dependent. This is true, for example, of many kinds of conflict (Maynard Smith

and Price, 1973) and reciprocity (Trivers, 1971). Evolutionary game theory (Maynard Smith, 1982) was developed as a framework in which to analyze such situations where there is technically no "optimum" at all. Instead, there is usually an "unbeatable" phenotype (or mixture of phenotypes) that resists invasion by others. As was mentioned earlier, sex ratios also fall into this category, and they were explicitly recognized as having a game-like character by Hamilton in 1967. Sex-ratio evolution has also developed into a huge, multifaceted field of research that exemplifies many features of the optimization approach.

Foraging was one of the first kinds of behavior to be treated explicitly as an optimization problem (Emlen, 1966; MacArthur and Pianka, 1966; Schoener, 1971; Charnov, 1976; reviewed by Stephens and Krebs, 1986), and in many respects it remains the "classic" application of the approach. It involves a wealth of straightforward, realistic trade-offs that are usually not frequency dependent (e.g., size of prey items *versus* the time needed to find or retrieve or process them), and it has been extremely successful in helping to elucidate the constraints under which animals operate in attempting to secure nutrition for themselves and their offspring. Indeed, its success has been so great that the words "optimal" and "foraging" have fused in many peoples' minds, producing a new term, "optimalforaging," that denotes what animals do when they get hungry.

What do all these applications of optimization have in common? One answer is that they are about phenotypes of a kind that did not concern the Reverend Paley. Habitat-patch selection rules, numbers of eggs in a clutch, and age-specific schedules of growth, fertility, and mortality are not like watches. They do not shout "Look here! I'm an intricate, improbable, and therefore onerous *adaptation*! Explain me if you can!" Darwin's puzzlement about the sex ratio derives from his realization that it must be subject to selection, even though he could not see how to assess the adaptedness of a given ratio of males to females among the progeny of a reproducing individual.

Little theory is needed to recognize that the vertebrate eye embodies a great deal of adaptation. Here the problem (and the main purpose of theory) is to explain the manifest adaptation of the eye. A sex ratio, on the other hand, is not obviously a problem at all. We need theory to reveal the problem, by explaining in what ways sex ratios might be adapted (Thornhill, 1990). In other words, an important difference between eyes and sex ratios is that the presence of design is obvious for eyes but not for sex ratios, where the initial problem is to find a way to recognize the presence of design and to assess what would constitute a more or less well-designed sex ratio. Much the same can be said for most of the examples discussed above, and others like them, where the role of theory is subtly but importantly different than in examples like that of the eye. Of course optimization approaches can be used (and have been used) to study the designs of eyes (Goldsmith, 1990) and other structures from molecules through organ systems of many kinds, to the shapes of entire organisms. But optimization models serve significantly different functions in the two kinds of situations, and they tend to play much more central and conspicuous roles in the analysis of sex-ratio-like phenomena than they do in the analysis of eye-like phenomena.

## V. The Aims and Limits of Optimization

For convenience and for the sake of brevity we have tended to speak of "the optimization approach" as though it were a well-defined method that could be applied in much the same way to almost any problem in the analysis of adaptation, but of course this is not so. In some applications, the approach amounts to little more than asking pointed questions about the selective regime and the potentially important constraints: What's the function of this structure? How does the observed variation in its form affect the fitnesses of individuals? Why does it take slightly different forms in different species, and in the sexes? Are there costs involved in producing different forms of the structure? Do the costs vary with environmental circumstances? What historical legacies might be limiting the range of accessible variation? And so on. At this level, the approach is mainly heuristic and could be described simply as "thinking like a biologist." Answers to the questions are plainly speculative and would never be viewed as more than guides to further empirical description or experimentation. Of themselves, they would never be mistaken for results or conclusions.

But when we move beyond this rather casual level of thinking about the evolution of an interestingly constrained phenotype that varies and that might have significant effects on fitness, and begin to construct more formal, mathematical models that identify specific optima as functions of given parameters, the relationship between an optimization model and a scientific belief becomes much more confusing. Of course a model is just a model, and the world is the world. But we cannot simply leave it at that because the whole point of the exercise is to use models to illuminate the world. How is this connection to be made, and how do we know what we have learned as a result?

A standard answer (suitable for scientists if not philosophers) is that models are intentional caricatures or cartoons, whose purpose is to help us strip away irrelevant complications so as to gain some insight about how a small number of key variables might interact. On this view a model is literally a toy world that we can manipulate and dissect in ways that we cannot directly manipulate or dissect the real world. Having understood the behavior of the toy world, we can ask whether it seems to mimic the real world in ways that suggest it embodies (in its highly abstracted and simplified way) interactions *like* those that occur in reality. To the degree that we persuade ourselves that it does, and that the modeled interactions are general, we have learned something potentially important about how the world might actually work (see Levins, 1966; Beatty, 1980; Grafen, 1991).

But can't we do better than this? Can't we validate models by testing their predictions? This is where the trouble begins because the answers are not straightforward. An optical model of an eye might be tested decisively because it embodies a fairly complete description of those aspects of the system at issue and because all of its parameters can be estimated directly. Such models have in fact been constructed and used to show that the vertebrate eye achieves a remarkably large fraction of its theoretical maximum optical efficiency on various measures of performance (Goldsmith, 1990). This is fascinating, but it does not answer the kinds of questions we are likely to be most interested in as students of the evolution of adaptation. After all, vertebrate eyes would still

seem almost miraculous (and Paley's arguments would be just as important, qualitatively) if they were only 10% or even 1% efficient. Models that address the questions we are most concerned about, as evolutionists, are generally not subject to such decisive tests because they do not incorporate all the relevant parameters, or because not all the parameters can be estimated accurately, or both.

What, then, are the questions we hope to answer with the help of optimization models? It is sometimes stated that such models are made on the assumption, or for the purpose of showing, that the phenotypes under study are "optimal," or that natural selection produces optimal adaptations, or that all of the characteristics of organisms are adapted (e.g., Lewontin, 1978, 1979, 1984; Gould and Lewontin, 1979; Dupré, 1987; Orzack and Sober, 1994a,b). This "program" is often referred to as "adaptationism." In fact, the aims of real optimization studies are rarely to see how close a phenotype is to its optimal state. Herre's (1987) study of sex-ratio adjustment in 13 species of fig wasps is one of the few examples we know of (Fig. 4). Here the model can be assumed to capture the relevant biology with enough quantitative accuracy to allow the fitness consequences of a given sex ratio to be evaluated. And for reasons
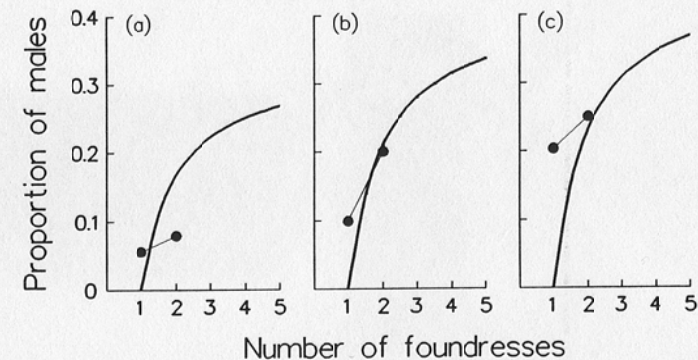


**Figure 4**  Predicted and observed sex ratios for three species of fig wasps in Panama. The species pollinate (a) *Ficus paraensis*, (b) *F. popenoei*, and (c) *F. trigonaia*. In (a), 97% of all figs contain the offspring of just a single female. In (b), 36% of broods are from single females. In (c), only 7% of broods are from single females. The solid curves show predicted ESS sex ratios for each species as a function of the number of foundresses contributing offspring to the mating group inside a fig. The curves differ slightly due to differences in the average intensity of inbreeding in the three species. The filled circles show *observed* sex ratios in single-foundress and two-foundress figs. Note that in (a) and (c) mother wasps produce sex ratios near the prediction in the kind of fig they more often encounter, but not in the kind of fig they seldom encounter. However, in (b), a species that frequently encounters both single-foundress and two-foundress figs, sex ratios are fairly near the predicted ESS in both conditions. This suggests that selection in (a) and (c), has been too weak to maintain an appropriate sex-ratio response to a situation that females seldom encounter. Ten other species of fig wasps were studied in the same way. On average, the magnitudes of the adjustments made by females of a given species were positively related to the variance of foundress number in the field, consistent with the hypothesis that the precision of an adaptation such as this sex-ratio adjustment (which is absolutely advantageous in all species) will be higher in species that gain more from making precise adjustments than in species that gain less because they less often encounter figs with foundress numbers different from the mean for their species. Redrawn from Herre (1987) courtesy of the author and *Nature*.

explained in the figure legend, "how close" is a genuinely interesting question in this case. However, this is not a typical use of optimization models. The hypothesis under test is usually not that a phenotype is optimal, but instead that the specific assumptions embodied in the model (e.g., the sources of selection, and the constraints) could account, at least in principle, for the evolution of the phenotypes under study (see Parker and Maynard Smith, 1990). "The role of optimization theories in biology is not to demonstrate that organisms optimize. Rather, they are an attempt to understand the diversity of life" (Maynard Smith, 1978).

Formal optimization models figure prominently in the study of allocation of nutrients, time, and other resources to growth, reproduction, and other activities, but for several reasons they figure less prominently in the study of structures such as eyes. As we mentioned earlier, such models provide a means of detecting and evaluating the designed features of allocations, which are processes rather than architectures in the usual sense. In addition, such allocations often involve well-defined trade-offs that lend themselves to mathematical analysis. Allocations are also usually continuous or nearly continuous quantitative traits that can reasonably be expected to be under polygenic control and sufficiently heritable to permit their evolution in any relevant direction, if subject to selection. And most importantly, the kinds of allocations studied in this way are usually closely connected to fitness, so they can be assumed to be subject to fairly strong selection. Thus attention can be focused on attempting to understand the nature of that selection and of the constraints that modulate its effects. If a model is constructed and found to give a poor fit to data, suspicion reasonably falls on the model's specific biological assumptions, not on the assumption that the allocation affects fitness. Under these circumstances, the purely phenotypic and relatively ahistorical optimization approach makes sense, and it demonstrably works.

There is more to the diversity of life than resource allocation, of course. Optimization models will remain relatively unimportant in many areas where the diversification we seek to understand involves evolutionary transitions of a relatively qualitative kind, or where selection was not the dominant evolutionary force, or where there is no natural way to parameterize the trade-offs of interest in a common currency. In such situations optimization analyses may be impossibly difficult or simply beside the point. Even within a single complex structure or behavior, certain features may show clear evidence of optimization that can usefully be studied with the aid of formal models, while other features show little evidence of optimization and resist such analysis. For example, the vertebrate eye is stunningly optimized in some respects, yet it also has features that are conspicuously nonadaptive or maladaptive, as illustrated in the following passages from Williams (1992):

As [Paley] claimed, the eye is surely a superbly fashioned optical instrument. It is also something else, a superb example of maladaptive historical legacy. The retina consists of a series of special layers in the functionally appropriate sequence. A layer of light-sensitive cells (rods and cones) stimulate nerve endings from one or more layers of ganglion cells that carry out initial stages of information processing. From these ganglia, nerve fibers converge to form the main trunk of the optic nerve, which conveys the

information to the brain. All layers are served by blood capillaries that provide their metabolic requirements. Unfortunately for Paley's argument, the retina is upside down. The rods and cones are the bottom layer, and light reaches them only after passing through the nerves and blood vessels. ... That we do not ordinarily perceive these shadows [cast by the larger blood vessels] is the result of minute involuntary eye movements, which keep the blood-vessel shadows moving, and of our brains recording the flux of images as continuous pictures. The reality of the shadow of the *vascular tree*, and the seriousness of the problem it presents, can be demonstrated with a flashlight and instructions from a visual physiologist.

Williams describes some other "stupidly designed" features of the vertebrate eye, and then offers a historical scenario that shows how our presently maladaptive retinal orientation seems to have been assembled, in a sequence that could have been driven by optimizing selection at every step.

The vertebrate eye originated in a tiny transparent ancestor that had no blood corpuscles and formed no retinal images. The retinas arose as light sensitive regions on the dorsal side of the anterior end of the nervous system. Evolutionary conversion of a flat to a tubular nervous system put the future retinas inside. In subsequent evolution, the photosensitive layer pushed outward from the brain to become part of the complex optical instrument known as the eye. All through history this layer has retained its position beneath the other layers of the retina. ... Unlike that of a vertebrate, the retina of a squid is right side up. Molluscan eyes evolved independently of vertebrate eyes, and show an entirely different suite of historical legacies. (Williams, 1992, pp. 72-74)

In summary, the outlook and techniques of optimization modeling are applied most often and most profitably to the analysis of phenotypes that involve the "allocation" of a continuous or nearly continuous "resource" of some kind to several "competing" activities with direct effects on fitness. Such phenotypes tend to show clear-cut trade-offs and continuous variation in parameter values. They can be modeled in fairly natural ways, are typically subject to strong selection, and are expected to respond in appropriate ways to such selection.

## VI. How Do We Know What Matters and What Is Feasible?

When we considered the evolution of clutch size in birds we did not even ask whether we had found appropriate definitions of the actor (parent birds), the strategy set (any number of eggs from 1 to $n$), and the objective function (the number of offspring surviving to reproductive age). The analysis was equally straightforward: find the number of eggs $n^*$ that maximizes the number of offspring that survive to one year of age. We did not worry about these matters because they seemed obvious, and because after we took account of a few important complications such as parental variation in condition, the result was a coherent and seemingly correct (or approximately correct) explanation of how one group of birds regulates clutch size. But there are cases in which these

central elements of the model are not so easily identified. Indeed, a major purpose of optimization modeling is often to help answer the questions posed by the title of this section.

When two or more imperfectly related actors are involved in a common endeavor, their optima may differ. For example, if the eggs already laid in a clutch were allowed to decide when their parents should stop laying, they would usually have the parents settle on a smaller clutch than was optimal from the parents' point of view because each egg values its own future reproduction more than that of its siblings. At some point adding an additional sibling would reduce each egg's expected fitness (by reducing its fledging weight) more than it would contribute indirectly through the sibling's reproduction. Of course it is hard to imagine an egg imposing its will on a parent, but hatchlings can interfere with each other in ways that advance their interests at the expense of the interests of their siblings and their parents (e.g., Godfray and Parker, 1991; Mock and Parker, 1996).

There are many other situations where *parent-offspring conflict* (Trivers, 1974) implies that an allocation or other decision will not be optimal for some members of a family. For example, in many social Hymenoptera the equilibrium sex allocation is 1:1 from the queen's point of view, but female biased (up to 3:1) from the workers' point of view, due to the workers' closer genetic relationship to the colony's female reproductives than to its males (Trivers and Hare, 1976). A pattern of biased allocation ratios supports the view that the interests of workers largely prevail in many species. This model has been extended in various ways. For example, one extension predicts that bimodal sex-ratio variation should sometimes occur among colonies within a species as a response by workers to inter-colony variation in the magnitude of the relatedness asymmetry (Boomsma and Grafen, 1990). Both the prediction (bimodal sex-ratio variation) and the assumed causal factor (relatedness variation) have been confirmed in several species of ants (e.g., Sundström, 1994; Evans, 1995) (see Fig. 5).

A mammalian infant is imperfectly related to its mother and its present and future siblings, and it was equally imperfectly related to them as a fetus *in utero*. There is, as a consequence, no reason to assume that the intimate physiological relationship between mother and fetus will be purely cooperative and "optimally" designed for the efficient production of a healthy neonate, although this has long been an accepted view. Once it is appreciated that what is optimal for the fetus may differ from what is optimal for the mother (with respect to at least some aspects of the relationship), then evidence of pervasive design for conflict, on both sides, begins to emerge from a critical reevaluation of fetal and placental development and physiology (Haig, 1993 and personal communication).

There may even be conflicts within a fetus, between the maternally and paternally inherited halves of its genome, stemming from the unequal genetic relationships of maternally and paternally inherited genes to their homologs in siblings of the fetus (Haig, 1992). Thus the optimal pattern of fetal gene expression may frequently differ for genes inherited maternally and paternally. Differential gene expression of the expected kind appears to occur in diverse taxa, mediated by the mechanism of genomic imprinting (Haig and Graham, 1991).
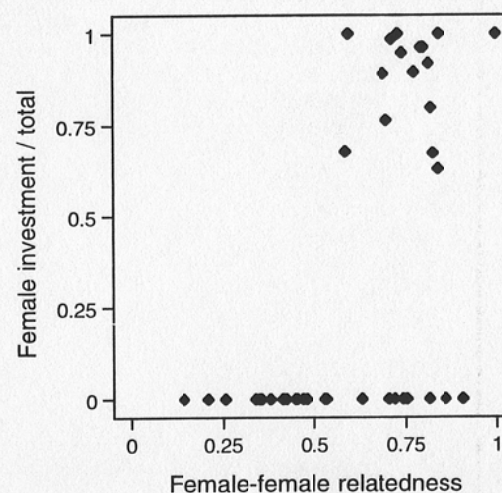


**Figure 5** Proportional investment in female reproductives as a function of the average coefficient of relatedness among females within nests of the facultatively polygynous ant *Myrmica tahoensis*. Only nests with high relatedness (on average, near the maximum possible value of 0.75 for outbred haplodiploid full sisters) produced female reproductives, and if they did so, they produced *mainly* female reproductives. All nests with average relatedness coefficients below 0.5 and some with higher values produced only male reproductives. In this species, the considerable variation in average relatedness within nests is caused almost entirely by variable numbers of variably related queens; most queens mate with just one male, so all their daughters are full sisters. Redrawn from Evans (1995).

It is ironic that the "optimization" approach to the study of adaptation has revealed a wealth of irreconcilable conflicts of interest that often give rise to wasteful squabbles. Conflicts of interest tend to be noticed by investigators pursuing the optimization approach because the approach demands that actors and objective functions be explicitly identified.

In situations where the relative fitnesses of alternative phenotypes are frequency dependent, the appropriate objective function may not be subject to optimization in the usual sense. As was mentioned earlier, this often occurs in situations involving conflict, mate choice, mimicry, sex allocation, and other interactions where rarity tends to be advantageous. In these situations, optima are replaced by *evolutionarily stable strategies* (ESS) (Maynard Smith and Price, 1973), which are phenotypes or mixtures of phenotypes that cannot be invaded by other members of the strategy set. The ESS is often absolutely worse, for all actors, than another more "cooperative" equilibrium would be, but the cooperative equilibrium is evolutionarily unstable because it is subject to invasion by "defectors." The formal game most often used to illustrate this point is the prisoners' dilemma, in which both parties stand to gain the highest fitness by cooperating, and the lowest by defecting, but defection turns out to

be (tragically) the only ESS (Maynard Smith, 1982). Balanced sex ratios are often tragic in a similar way. For most species in which males do not help to rear young, the species would do best if it had a strongly female-biased sex ratio because its potential rate of population increase is a function of the number of females, not the number of males. But such globally "optimal" sex ratios do not persist because they can be invaded by genotypes that incline their bearers to make only male offspring. What, then, is the sex ratio a design for doing? This question repays careful thought.

Sex-ratio evolution stumped Darwin because he could not identify an appropriate currency and objective function. Fisher's breakthrough was to realize that for purposes of this problem, there is a qualitative difference between "number of children" (which does not lead to a correct analysis) and "number of grandchildren" (which does, at least in most cases). With this key insight about how to assess the fitnesses of alternative phenotypes, and with an appreciation of frequency dependence, sex allocation suddenly becomes understandable. It has provided rich opportunities for successful application of the optimization approach because the trade-offs involved tend to have large effects on fitness and because the key variables can often be estimated fairly directly (see Charnov, 1982).

The most appropriate measure of fitness is seldom as easy to define as it often is for problems like clutch size and sex allocation. For example, theorists concerned with the evolution of senescence and related life-history phenomena have spent much effort trying to understand how measures such as age-specific intrinsic rates of increase can be used to evaluate the relative long-term fitnesses arising from life-history parameters in age-structured populations (see Rose, 1991; Charlesworth, 1980, 1994). Fitness can also be remarkably difficult to measure in temporally varying environments, especially for age-structured populations. Cohen showed in 1966 that partial germination of seeds could be favored by selection in annual plants that experience drastic year-to-year variation of environmental quality, when doing so maximizes their geometric mean fitness (reviewed by Seger and Brockmann, 1987; Philippi and Seger, 1989). But no similarly general fitness measure for age-structured populations (e.g., perennial plants) has yet been discovered. Some recent theoretical explorations suggest that age structure in the context of temporal variation may sometimes support unexpectedly complex polymorphisms involving "quantized" alternatives (Sasaki and Ellner, 1995; Ellner and Sasaki, 1996). Such findings would undoubtedly be easier to explain if we understood at a fairly general level how to construct natural objective functions for these kinds of populations.

The objective-function problem becomes even more difficult where the phenotypes under study are "performances" (such as that of the eye) that cannot easily be tied to fitness in a quantitative way. In such cases it may be almost impossible to parameterize the costs and benefits realistically. What is the cost of making a certain bone slightly thicker and thereby stronger? What exactly is the benefit? It may be possible to frame the issue in qualitative terms (e.g., a thicker bone will decrease maximum running speed and impose increased energetic costs of transport), but even where these functional costs can be estimated empirically, there is no obvious way to map them onto fitness differences. Without such a mapping, it is impossible to estimate the trade-off

structure under which optimization is expected to take place. [See Chapter 2.]

As a consequence of this problem, the optimization approach tends to be applied in a different way to phenotypes relatively far removed from reproduction (for example, many aspects of morphology) than it is to clutch sizes, sex ratios, and the like. Where realistic, fully parameterized models cannot be constructed, the approach tends to emphasize induction from comparative data rather than hypothetico-deductive reasoning from first principles. For example, many comparative morphologists and physiologists are now concerned with fascinating questions about margins of safety in the design of organ systems that may fail catastrophically under unusually heavy loads that occur only rarely, if at all, in the life of a typical individual. "Excess capacities" should certainly be subject to optimization if they cost anything, which they undoubtedly do. But to estimate those costs directly would be extremely difficult if not impossible. However, where the excess capacities can be measured their allometries can be studied comparatively (e.g., Niklas, 1994a,b), and the resulting patterns can be used to refine hypotheses about the evolution of safety factors. In cases such as this, optimization modeling is more heuristic than analytical, but it may nonetheless be valuable as an agent of biological intuition and imagination, and it may thereby contribute to the refinement of the questions addressed by empirical research.

One of our favorite examples of a good question derived from heuristic optimization reasoning concerns the relative testis sizes of primates. Like many kinds of structures, testes show regular allometric relationships with body size, but not all species lie close to the line describing the overall trend of the data. Harcourt et al. (1981) decided to ask whether the deviations might be explained, in part, by variation in the mating systems of the species. What made them ask such a question? They realized that in species where estrous females commonly mate with more than one male, the fitnesses of males would be determined in part by sperm competition. Thus, other things being equal, males that produced large quantities of sperm should realize larger benefits from doing so in such species than in those where females typically mate with only one male. If sperm production were costly, then the optimal level of sperm production would be higher in species with multi-male social groups than in monogamous species and harem-polygynous species such as the gorilla. On the assumption that testis size and sperm production are correlated, Harcourt et al. reasoned that multimale species should tend to fall above the average allometric relationship (with testes large for their body sizes), while single-male species should tend to fall below the line. This is exactly what they found. The result is of interest for many reasons, including that it shows how different aspects of sexual dimorphism may exhibit very different patterns of association with each other and with ecological and social variables (see Harvey and Harcourt, 1984). For example, male gorillas are large and "masculine," both absolutely and relative to female gorillas, but they have testes that are absolutely and relatively tiny. Similar patterns occur in other taxa such as whales (Brownell and Ralls, 1986). For example, right whales have a spectacularly promiscuous mating system, and they have the largest testes recorded for any animal (both absolutely and relatively, at more than 1% of body mass). The mating systems of most large whales are unknown, so whale biologists interpret the observed allometric deviations as hints about the

patterns of behavior to be expected in these species.

The difficulties involved in defining the actors and objective functions may sometimes be substantial, but they are seldom as great as those involved in defining the constraints and strategy sets. One problem is that the constraints are of many different kinds that are not always clearly distinguished. For example, many physical and ecological constraints correspond fairly closely to those that arise in engineering, but there are other, more "internal" developmental and genetic constraints that reflect historical legacies of a kind that loom much larger in biology than they do in engineering, where it is often possible to "leap" from one peak to another in the adaptive landscape. Evolution can only "tinker" with what already exists (Jacob, 1977). If a lineage is to survive then there must be a continuously viable and selectively favorable path between each successive state of any phenotype that is subject to even moderately strong selection. This pervasive dynamical constraint is at the root of many others in biology, but it has only weak analogs in engineering. The jet engine did not evolve gradually from the reciprocating engine, nor did the 747 evolve gradually from the Wright brothers' flyer, least of all in midair! Yet this is equivalent to what organisms do routinely. Among the consequences are "stupid" designs like those of the vertebrate retina, as described above.

Historically derived developmental and genetic constraints are of special concern because they may give rise to hidden components of the trade-off structure that prevent a phenotype from evolving in a direction that we might otherwise reasonably expect to see. The existence of such a constraint may be suggested by a striking lack of intra- or interspecific variation. For example, the number of cervical vertebrae is highly variable across tetrapods as a whole, but in some groups the number is remarkably constant. All turtles appear to have exactly eight cervical vertebrae, even though the necks of turtles are very diverse in other respects. Similarly, all mammals have seven cervical vertebrae, except for manatees (six) and three-toed sloths (eight or nine). Even "neckless" mammals such as whales and dugongs, and long-necked mammals such as giraffes, have seven. Why such constancy? It seems very hard to believe that eight is currently optimal for all turtles, and seven for almost all mammals from shrews to whales. Indeed, there are reasons to think that other numbers might be of great value to some turtles or mammals. Sloths exhibit an owl-like ability to rotate their heads through almost a complete circle, and a similar range of motion might well be of advantage to many other mammals. But there is evidently something about the developmental programs of turtles and mammals that makes it very difficult for the number of cervical vertebrae to change. Not all tetrapod groups show such conservatism. For example, the plesiosaurs included species with short necks and few vertebrae (e.g., 13 in *Brachauenius*), and others with elongated, flexible necks and many vertebrae (e.g., 76 in *Elasmosaurus*) (Romer, 1966).

Similar instances of extreme conservatism in some taxa and great variability in others can be found throughout the living world. For example, the parasitic Hymenoptera show a wide range of numbers of segments in the antennae, but all aculeate Hymenoptera (the familiar ants, bees, and true wasps) have 13 antennal segments in males and 12 in females. The only exceptions are a few species in which males, like females, have 12 segments. Again, it seems inconceivable that this pattern represents a uniform optimum, with respect to antennal function, for tens of thousands of aculeate species. Instead, it seems more likely that such patterns reflect other functions that impinge, in other ways, on the number of antennal segments. This can happen, for example, when particular structures or the developmental processes that give rise to them become necessary antecedents to the development of other structures that make an important contribution to fitness (see Maynard Smith et al., 1985). Thus the number of antennal segments may indeed be under stabilizing selection, but for reasons that have nothing to do with antennal performance as such. As a consequence, it may be more feasible to radically modify the sizes and morphologies of individual antennal segments (or cervical vertebrae, etc.) than to change their number.

In constructing a strategy set, it is important to ask whether the feasible phenotypic options may be limited (effectively if not absolutely) by deep-seated constraints whose origins and influence on the phenotypes of interest are less than obvious. Sometimes the existence of such unappreciated constraints is revealed by apparent "failures" of optimization. For example, annual plants seem to do some things exactly as optimization models say they should, such as adjusting their flower lifetimes in relation to construction and maintenance costs and the behavior of pollinators (Ashman and Schoen, 1994). But they chronically fail to show the kinds of sudden switches from vegetative growth to reproduction that simple life-history models often predict. This lack of fit between models and reality has led in recent years to the view that fundamental aspects of plant architecture and development may often make it most profitable for a plant to grow and reproduce simultaneously for much of the season (see Fox, 1992). Analogous temporal constraints on offspring production in bees may force a revision of standard models for the evolution of hymenopteran eusociality. These models treat reproduction as an instantaneous process, and for that reason proved unable to account for patterns of genetic relatedness within colonies of a very well studied sweat bee (Richards et al., 1995).

The principal goal of an optimization study is often, at least implicitly, to describe and understand the constraints and strategy sets. We want to know why organisms are limited in the ways they are, for example, to making their livelihoods only in certain ways, at certain places, and with finite lifespans. It is therefore no accident that the word "constraint" appears in the titles of increasing numbers of papers in which optimization approaches are used to study adaptation (e.g., Goldsmith, 1990; Partridge and Sibly, 1991; Arnold, 1992; Jones et al., 1992; Moran, 1994). Some constraints are highly particular and historically contingent, but others may be more or less universal. When the latter give rise to trade-offs that affect many species in similar ways, they may reveal themselves as allometric patterns in large-scale comparative data sets (e.g., Harvey and Pagel, 1991). The study of such patterns may lead to the discovery of general rules about important classes of trade-offs (for example, ones affecting particular aspects of life-history evolution) and hence, eventually, to a deeper understanding of the causes of the underlying constraints (Charnov, 1993).

## VII. Conclusions

Natural selection can be viewed as a process that evaluates alternative designs by increasing the frequencies of those that are better adapted for reproduction in the current environment. Students of adaptation mimic this process by constructing and analyzing optimization models. Such models are among the most drastic simplifications tolerated anywhere in biology, and they are sometimes criticized for this reason. For example, they notoriously ignore the issues of evolutionary dynamics entailed by the genotypic control of phenotypes. But this simplification serves an important function. By focusing attention on a few key aspects of the situation under study, it elicits questions that might otherwise go unasked. Genetic models are most productive when they connect genotypes to phenotypes in ways that make biological sense, for example, by embodying appropriate constraints and by not preventing unbeatable genotypes to emerge. Thus optimization approaches can be viewed as important components of genetic approaches to the study of adaptation (see Chapter 4).

Optimization approaches work best where the phenotypes under study can change without forcing many other aspects of the organism to change at the same time ("quasi-independence"; Lewontin, 1984). The "mysterious laws of the correlation of growth" troubled Darwin (1859) for the same reasons that they trouble modern students of adaptation, but in fact such correlations do not interfere, in the end, with many kinds of evolutionary change. It seems extremely interesting and important that real organisms are only modestly integrated in this sense; they show "natural planes of cleavage" among organ systems, biochemical pathways, life stages, behaviors, and the like, which are at least sufficiently smooth to allow some character states to respond to selection without too seriously degrading the adaptation of other character states. What determines where these planes of cleavage are located and how deep and smooth they are? For understandable reasons, biologists have long treated them as unfathomable "givens." We suggest that it may now be possible to begin working toward a "theory of organic articulations" that would give insight into the "laws of correlation." Genome sequencing projects are already allowing us to glimpse, for the first time, not only the outlines of complete genetic "parts lists" for entire organisms, but just as importantly, the histories of those parts. A few theorists have begun to ask questions about the spontaneous emergence of "subsystems" in abstract functional networks subject to adaptive evolution (see Kauffman, 1993), but it should soon be possible to add some realism to such models, and it should certainly be possible to ask experimentally whether certain kinds of maladaptive pleiotropies and genetic correlations tend to be selected downward and, if so, then to find out how the response was achieved. In short, we suspect that the early 21st century will see the emergence of a field of study focused on questions about the evolution of organ systems, networks of genetic regulation, and other aspects of the "partly compartmented" design of organisms.

While biologists were borrowing classical optimization techniques from economics and engineering, workers in those fields were turning to biology for the inspiration behind genetic algorithms, which solve optimization problems

by simulating evolution. This exchange should lead eventually to an enriched understanding of adaptation. Insights about the properties of successful genetic algorithms could illuminate the biological processes that inspired them. Genetic algorithms became interesting and practical after high-speed computing became widely available and virtually free. For biology, effectively unlimited computing power opens up the possibility of a previously impractical style of "experimental" theoretical study, in which model genetic systems underlying (initially) specified developmental systems are set up and allowed to evolve in large populations for very large numbers of generations. With increasing knowledge of development, we might come full circle and study adaptation by modeling the evolutionary process directly. For a long time we evaded the dynamical complexities of genetic evolution by reducing it to a black box with just a few parameters (as in quantitative genetics) or by simply assuming it away and directly optimizing the phenotypes themselves. Perhaps we will soon begin to understand at a deeper level why it has so often been possible to get away with this.

This chapter has pointed out repeatedly that few character states may ever be in truly "optimal" states, although most may be (metaphorically) "pursuing" optimality. If maladaptation is a chronic condition, shouldn't organisms be adapted to it? Could the phenomena long studied under the rubric of "developmental canalization" be manifestations, in part, of mechanisms that evolved to ease the burdens of imperfection?

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