Optimization in Ecology

Natural selection produces optimal results unless constrained by history or by competing goals.

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The Optimality of Natural Selection

As all important processes and patterns in biology are products of natural selection, it is somewhat tautologous to speak of optimization in a biological context. This is because natural selection is defined and operates as a mechanism that maximizes fitness, or the relative contribution of a genotype to future generations; it leaves only the best-adapted or optimal phenotypes for our inspection. A phenotype that performs optimally in current environments may have several genotypes, but ecologists are more interested in phenotypic traits, since these are more easily measured in the field, and since we generally have no knowledge of future environments that might distinguish between different genotypes with an identical phenotype.

If overall fitness is optimal in the sense that natural selection has been unable to produce anything better, how does its value compare to some theoretical optimum that might be gained in the best of all possible worlds? This distinction led Fisher (*1*) to his observation that, with time, mutations are increasingly likely to be detrimental, and to his "fundamental theorem," that rates of gene frequency change should be proportional to the genetic variance of the population. But it is possible that populations spend more time tracking moving fitness optima (that is, climbing the sides of shifting adaptive peaks on Sewall Wright's adaptive landscape) than they do sitting the summit optima. In fact, with two alternating environmental states (for example, seasons) selection may be close to producing an optimal phenotype in a short-generation species in one regime at the point a second environment takes over and in which fitness is minimal! This has been termed the Epaminondas effect (*2*), after the little boy who always did the right thing for the previous situation.

Leaving considerations of tracking variable environments aside, we pursue the distinction between the best available and the best possible phenotypes. The degree to which these differ will depend on various constraints. With overall fitness, the constraints of history and chance are likely to be important. For example, the best plant phenotype for survival in the driest deserts will exist only if the mutations that control water economy have actually occurred, and the plant will grow in a particular desert only if the chance mutants have actually dispersed from their points of origin. We could possibly avoid many of these historical constraints by looking not at overall fitness but at its various components. It might well be that overall fitness in a Mohave Desert succulent exceeds that in a Sahara Desert succulent (one plant would always out-compete the other, in either desert), but nevertheless they should be solving similar subproblems of a reduced moisture budget in similar (optimal) ways. Thus the way individuals are spaced in the desert, the patterns of root dispersion for rapid water uptake, the reduction of leaves and stomata and of surface-to-volume ratio, should all reflect in both deserts a common selection of different aspects of water balance and a common solution to the respective problems.

In general it seems that optimization in higher-order phenomena will be subject to a wider variety of constraints than in lower-order phenomena. I regard as higher-order phenomena the composition and organization of faunas and diverse communities, and contrast these to events at or below the level of the organism, an example of such an event being the organization of circulation systems. Apparently there are few constraints, in terms of competing goals or alternative energy drains or historical considerations, to optimal design in starfish arteries and leaf venation; such systems follow the same principle of branching angles being relative to duct sizes as applies to a well-built sewage system (*3*). On the other hand, at the level of single species populations, it is evident from simple demography how reproductive rate is maximized: lots of young, early and often. Yet reproduction takes energy, and there may well be competing energy drains, for other vital needs must also be met. The adult may be more likely to survive than its young, in which case it must be maintained in good condition so that it can again reproduce. Space or food resources must be defended against competitors, and the whole family protected from predators. With increasing number and importance of alternative and additional energy drains, it becomes increasingly less likely that what we predict in terms of maximal reproductive effort will be what we observe in nature. In contrast to the identity of optimum and maximum fitness, optimal and maximal reproductive effort are likely to differ, and overall fitness is maximized by a reproductive effort that is less than all out. A trend toward increasingly complex selective "fields" extends from lower through higher levels of organization such as communities and ecosystems, so that we will be able to label as "best possible" some facet of community or faunal structure with less and less certainty. It will simply be "optimal" with respect to the given constraints of history and a variety of simultaneous selective forces.

Tests for Optimal Solutions in Ecology

There are two different ways of testing for optimal solutions to problems of time- or energy-allocation in nature. The first is particularly valuable when the selective forces are likely to be many and various, and when it is therefore more difficult to reason a priori what the optimal outcome is likely to resemble. Let us take, for example, a grass field, which can provide seeds and insect prey for birds, and assume that the field is accessible to many bird species of a variety of morphological, ecologi-

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cal, and behavioral attributes. We can measure a number of variables in the resident bird community: number of species, types of species, and just how they use the field's resources. The question is: Are the values measured in any sense optimal? It can be answered by finding a similar field somewhere else, which is accessible to and has been colonized by a taxonomically or genetically different bird fauna. We now compare ecologies between fields both at the level of single phenotypes and of community makeup. If we find extensive similarities or convergences, we can infer that selection has reached optimal solutions in both fields, despite differences in history, time scale, and genetic origins.

I show the results of such a comparison in Table 1, in which a plot within a field equal to 10 acres (4 hectares) in central Chile is compared with one in Kansas (*4*). At the community level, each field supported three species, and resource division was accomplished in each field in very similar ways: in each field the three species differed chiefly in feeding behavior and bill structure, somewhat in habitat use, and little at all in the heights at which they fed. At the species level, the birds are matched one-for-one with striking morphological parallels; the first pair of species counterparts are taxonomically related at almost the genus level (*5*), the second pair only at the family level, and the third pair are in different families. It seems to matter very little to this outcome that, while the Kansas grassland is a natural one, the Chilean field is irrigated and can only have existed as a habitat type in central Chile since colonial days. Thus there is reason to believe that there is a single optimal way of dividing up the resources of this type of field, and that it has been achieved, or at least approximated to the same extent, on both continents.

This convergence in species and community structure extends well to other field and health habitats in Europe, and in North and South America (*4, 6*). But if one attempts to make such comparisons in more complicated habitats, or to compare higher-order patterns such as bird distribution over habitats, the parallelism breaks down and correspondence diminishes. Thus there are more bird species in matorral, a broad-leafed scrub habitat in the mediterranean zone of central Chile, than in the Californian equivalent, chaparral. And Chilean *Nothofagus* forests [and similarly those of Argentina (*7*), Australia, and Tasmania], support only about half the number of bird species as north temperate beech forests (*Fagus*), in spite of the similarities in vegetation structure. And finally, a comparison on a countrywide scale reveals an even more striking difference between Chile and California. Although these two places have similar areas, topographies, and similar total numbers of land bird species, bird species in Chile replace each other with geographic area rather than between different habitat types. In California the reverse is true, for a marked species turnover occurs between habitat types while little at all occurs between geographic areas in the absence of a habitat change (*6, 8*).

It is clear that this method of testing for optimal solutions is feasible only when history and chance provide genetic differences among geographic areas, but do not restrict the overall species diversity. An alternative and perhaps more direct test is to contrast what we find in nature to what is predicted a priori on the basis of models designed to mimic the essentials of the natural system. Based on little more than logic, such models operate by the selection of an optimum or limit by means of either geometry or differential calculus, such that fitness or energy income or numbers of offspring are maximized, or cost or energy or time expenditure are minimized. First I shall discuss a powerful general model with potentially wide applicability, then I shall describe models that apply to only one component of fitness.

"Strategic analysis" was initially used by Levins (*9*) to select optimal genetic makeup of populations in varying environments. The model identifies optimal phenotypes by a graphical process similar to that used in economics and in some decision theories, and is illustrated in Fig. 1. Suppose an environment contains two resources X and Y (or contains two types of habitat patch). The environment is called "coarse-grained" if an organism can take one resource preferentially over the other, or "fine-grained" if the resources must be used in the proportions in which they occur in the habitat. I will consider only the latter situation. For each resource there is a phenotype with optimal fitness, $\phi_{X,Y}$, and phenotypes can be ranked along an axis so that fitness falls monotonically from these optima, in a way often but by no means necessarily depicted by Gaussian curves. Each phenotype in the ranking (see upper left of Fig. 1) has a fitness on both resources, W_X, and W_Y, and can thus be represented in the plane of W_X and W_Y as a single point. The set of all possible phenotypes on this plane (upper right of Fig. 1) comprises the fitness set, from which the optimum phenotype is to be selected. This optimal phenotype is chosen for a particular environment, a mix with proportion

Table 1. Comparison in vegetation structure and bird species between a Kansas and a Chilean field.

Comparison	Kansas	Chile
Vegetation structure		
Mean height (meters)	0.29	0.27
Vertical density (number of leaves)	5.10	6.23
Horizontal density (number of leaves per meter)	8.68	9.26
Area under foliage profile	32.4	39.2
Bird community characteristics		
Number of species	3	3
Average between-species overlap in		
Habitat	0.63	0.60
Feeding heights	0.78	0.89
Food and feeding behavior	0.18	0.21
Overall ecology	0.53	0.56
Bird species characteristics		
Eastern meadowlark and red-breasted meadowlark (*Sturnella magna* and *Pezites militaris*)		
Body size (millimeters)	236	264
Bill length (millimeters)	32.1	33.3
Ratio of bill depth to bill length	0.36	0.40
Grasshopper sparrow and yellow grass finch (*Ammodramus savannarum* and *Sicalis luteola*)		
Body size	118	125
Bill length	6.5	7.1
Ratio of bill depth to bill length	0.60	0.73
Horned lark and Chilean pipit (*Eremophila alpestris* and *Anthus correndera*)		
Body size	157	153
Bill length	11.2	13.0
Ratio of bill depth to bill length	0.50	0.42

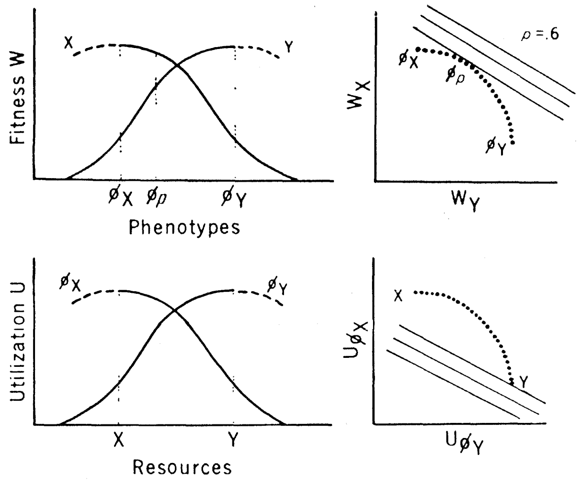

Fig. 1. The technique of strategic analysis. A range of phenotypes such as the bill sizes of insectivorous bird species has a fitness (W) distribution on each of two resources X and Y; likewise, a range of resources, such as sizes of insects, has a utilization (U) distribution by each of two phenotypes ϕ_X and ϕ_Y. The technique selects the optimal phenotype or optimal resource, given the mix p of resources used or phenotypes utilizing them.

p of X and $(1-p)$ of Y, by means of an adaptive function (indifference curve). Overall fitness has two components derived from the phenotype's encountering two resources, and is given by

$$\bar{W} = pW_X + (1-p)W_Y \qquad (1)$$

This is the equation of a straight line in the W_X to W_Y plane, and is the adaptive function, for a certain value p, which selects the optimal phenotype with maximal fitness $\bar{W}$. Its slope is given by $(p-1)/p$, and $\bar{W}$ is an index of the position of the adaptive function in the plane; the tangential intersection of fitness set and adaptive function at maximal $\bar{W}$ indicates the optimum.

Note that there is a duality between resources and phenotypes (species), and that the same system can select optimal resources, given the various utilization curves for phenotypes that live on them. The resource that receives the least use will presumably be able to grow at the expense of the others; this is selected by shifting the overall utilization

$$\bar{U} = pU_{\phi X} + (1-p)U_{\phi Y} \qquad (2)$$

by increasing the value of the constant $\bar{U}$ (a position index) until the fitness set of all X is intersected from below at the favored resource.

One of the reasons strategic analysis is such a useful tool in ecology is that it can be used in a very specific and quantitative way, or in a qualitative, conceptual fashion. I have used the concept to attempt to explain variation in clutch size of birds (*10*). Here the fitness set consists of phenotypes that allocate energy to alternative tasks in different ways. Because there are three obvious tasks: to reproduce, avoid predators, and repel competitors, the fitness set is a surface in three dimensions, and is most probably convex to the origin because (i) the total energy budget is finite and (ii) a little energy saved from a large reproduction (or other) budget will probably go a long way to boost low-budget competitive ability or predator avoidance. The adaptive function is likewise a surface in these three dimensions. It will probably be concave to the origin, because energy is allocated to alternative drains more or less sequentially. This means that its form will be

$$W_X{}^p W_Y{}^q W_Z{}^{(1-p-q)} \qquad (3)$$

which is a hyperbolic surface. These shapes are approximate but the theory does allow one to predict what will happen to the size of the energy budget for reproduction, of which one component is clutch size, when predator pressures vary, and when habitats become more crowded with both conspecific and allospecific competitors.

The method has proved useful to other workers. Wilson (*11*) has gained insight into the relative abundance of worker castes in ant colonies using strategic analysis. The colonies are faced with diverse tasks, such as caring for the brood, harvesting different food types, and defense; the ant castes, which differ in size and mouth morphology, show differing efficiencies in completing these tasks. Thus the fitness set comprises different relative caste abundances, the adaptive function varies with the task environment, and the optimal colony completes its chores with the minimal combined weight of worker tasks. MacArthur used the system for a parsimonious explanation of the evolution of sex ratios (*12*); optimal body size in hermit crabs can be predicted with the analysis (*13*); it has also been used (*14*) to illustrate the evolution of mimicry in butterflies.

Optimal Patterns in Spatial Distribution

It is often considerably easier to predict how an organism might obtain an optimal solution to one specific problem among the array of problems that it faces than to predict complete life history and life energy allocation. One problem on which it is relatively easy to collect data is how organisms space themselves. For example, creosote bushes (*Larrea*) grow in superficially uniform desert terrain where moisture availability is almost certainly limiting, and few if any considerations other than competition for moisture should affect spatial positioning. Researchers have looked for uniformity in the distances between the creosote bushes and their nearest neighbors, as young plants need access to a certain minimum area for their root systems in order to mature successfully and will survive only if they are spaced a certain distance from their neighbors. It is indeed surprising that this simple prediction has not been confirmed by the available evidence (*15*).

However, Yeaton, Thompson, and myself recently reexamined spacing in desert plants in general, and we found that in earlier investigations variation in bush size had not been taken into consideration (*16*). When the sum of bush sizes is plotted against their distance apart, a good positive correlation ($r = 0.7$, $P \ll .01$) results. An even more striking relation is obtained between bush size and the area of the polygon a bush is expected to drain of water. These polygons, which fill the plane of the desert floor, are formed by lines drawn normal to radii from each plant to each of its four to seven neighbors; these lines divide each radius into two lengths that have the same ratio as the ratio between the sizes of the bushes that the radius connects. Of course, "close packing" in two dimensions is by regular hexagons, which are the most rounded regular figures that completely fill the plane. It has similarly been found (*17*) that birds on uniform sandy beaches defend territories that closely approach hexagonal shapes. This means that the birds are defending areas optimally packed in the plane, consistent with uniform territory size and no interstitial space.

Rounded territories are optimal if an organism travels over the area to forage, and returns with food to some fixed point in the territory. Then its traveling time is reduced the more the territory becomes circular. I have examined the data from hawk foraging areas given by the Craigheads (*18*) and have found that very few territories deviate from circularity further than an ellipse with the major axis twice the minor axis, and that these deviations become even scarcer as territory size (and presumably traveling time) increases. One can further expect that territory owners will position their nests, to which food is being returned, as close to the center of a territory as site availability permits. Such a result has indeed been found, in grassland birds for which one might suppose an ample selection of nest sites exists (*19*); and we can take this result to further strengthen the hypothesis that traveling times are important, and should be minimized.

One can capitalize on the implication of traveling times in an interesting way, to answer the question: When should a territorial organism exclude from its territory not only conspecific individuals but also individuals of other species? Imagine first two bird species, each of which divides up a woodlot into territories that overlap completely with those of the other species. The same overall density of the two species can be achieved in another arrangement if each shrinks its territory to one half the former size, and defends it against all other birds of both species. The number of young that can be reared under the first arrangement is assumed to be proportional to territory size, food density, and time spent foraging, where the last term is some constant minus traveling time and is proportional to the radius of the territory (*20*). Under the second arrangement, territory size is halved, but food density is increased by a factor $(1 + \alpha)$, where α is an index of diet overlap between the two species; traveling time is reduced. When is the second arrangement more profitable? The answer is derived (*20*) in terms of the two variables r, territory radius, and α, diet overlap, and is summarized in Fig. 2A. For large values of α, species should defend territories interspecifically regardless of their size, but as α decreases, interspecific territoriality becomes advantageous only with larger and larger territories. With the ratio between the bill lengths of two species being used as a crude index of α, the pairs of bird species that are known to be interspecifically territorial are plotted in Fig. 2B. The correspondence with the model's prediction is convincing.

Optimal Diet Breadth

The second topic I shall discuss has already received a great deal of attention from theoretically inclined ecologists. The question to be answered is: Given that an organism faces a broad range of possible food items which vary in the case with which they can be found and captured and in their nutritional value, how can the organism feed optimally? In this case there are two solutions: the organism can feed so that it maximizes energy intake for a particular foraging bout, or it can restrict its diet for a certain energy intake and minimize the time it spends foraging. But, one can say, optimal diets result in optimal fitness in both cases. I will describe briefly four different approaches to this problem and, because the results are all very similar, show how they may be derived in a perhaps more general and versatile way.

Optimal diets can be investigated by means of the strategic analysis technique just described (*21*). Alternative diets are represented as points in the plane (quantity of resource X harvested per unit time) and (quantity of resource Y harvested per unit time); the outer boundary of the set of all possible diets obtained by substituting one resource for the other comprises the "fitness set." There is a certain set of diets which to the forager are equally acceptable; these comprise an "indifference curve," concave to the origin and equivalent to Levins' adaptive function. The model can predict how diet should change with changes in (i) resource density and (ii) the degree to which one resource can be substituted for the other. In another approach, MacArthur and Pianka (*22*) considered the cost to foraging as the sum of pursuit time and search time. Potential prey items are ranked 1,2, . . . n in terms of ease of capture, so that mean pursuit time increases with diet breadth. At the same time, if more food items are regarded as acceptable, then an acceptable food item is more easily found. Thus mean search time is a decreasing function of diet breadth. Therefore the search time and pursuit time functions of diet breadth intersect at some value j that is less than n, and the optimal diet includes all the food items to the left in the ranking, 1,2, . . . j. The model predicts that factors which reduce the search time (such as increased prey density) or increase the pursuit time (such as more elaborate defense mechanisms in the prey) will reduce the optimal diet breadth, and vice versa.

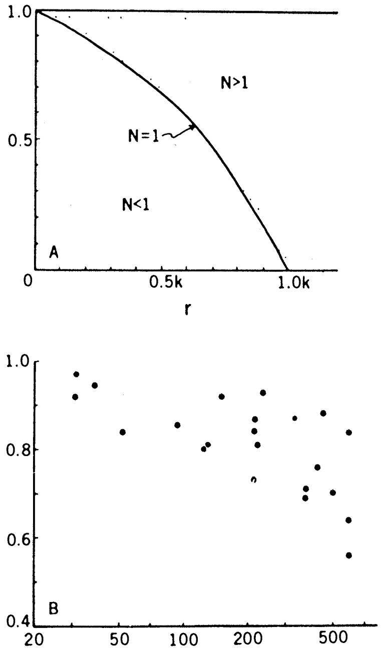

Fig. 2. (A) Diet similarity α is plotted against territory radius r. A simple model predicts that if two birds of different species have territory sizes and diet similarities such that they lie inside the stippled part of the plane, they should become interspecifically territorial. (B) Each point represents two birds of different species that are known to be interspecifically territorial. The supposed constant k of the abscissa in (A) becomes empirically a function of r in (B). Units of r are in feet (1 foot = 0.3 m).

Analyses of cost versus benefit have been applied to the problem of optimal diets. In a simple analysis of this type one examines the ratio of E (energy gained) to T (time spent). If a forager with a net time-energy balance E/T encounters a food item which yields energy e at a cost t, then the item should be eaten if $(E + e)/(T + t) > E/T$. If the caloric rewards of this food item are small compared to those from other food items in the environment, or if the time taken to capture and eat the item would be large compared to the time required to find a more worthwhile food item, then the inequality (above) is unlikely to hold and the predator should move on to look for other types of prey (*23*). A more general analysis is given by Schoener (*24*), who has written an extensive review of optimal feeding strategies. The basic model he considers is as follows. Energy is accumulated with increased time spent foraging, but at a decreasing rate. Organisms profit

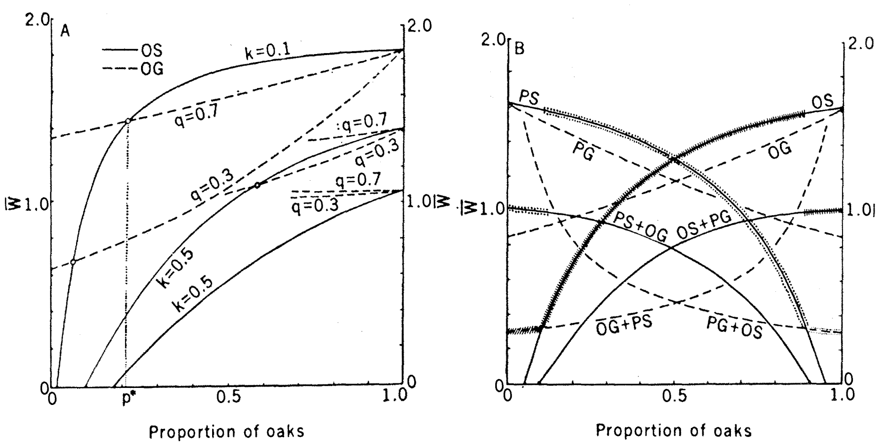

Fig. 3. (A) The fitness W of a bird that prefers oak trees for foraging decreases from right to left as the proportion p of oak trees in the habitat decreases. If the bird specializes on oak trees (OS), fitness drops gradually at first and then precipitously, but if it is a generalist (OG) in that it also uses the second tree, pines, its fitness drops rapidly at first but then levels out. The two curves (for a given value of tree similarity, q, and tree spacing, k) intersect at a critical value of p, p^*, such that to the right the species should behave as a specialist and ignore pines, but to the left should use both trees. (B) The behavior of two bird species, one adapted to pines and the other adapted to oaks, when they occur together on the pine-oak gradient. The data are for a k value of 0.3, a q value of 0.4, and a W value of 2; p^* is given by $k \ln W/(k-1) \ln q$, which in this case is 0.22. The curves PS and PG (pine specialist and generalist) and OS and OG (oak specialist and generalist) are for fitnesses without competition. The remaining curves are for species fitnesses in the presence of competition. The pine adapted species behaves as a specialist until the proportion of oaks is 0.89, and then switches to a generalist mode; the oak-adapted species specializes on oaks until the proportion of oaks is 0.11, when it also changes to become a generalist. See text for details.

by spending time doing other things besides foraging, for example, nest building and preening, and (net energetic) benefits lost because these alternative jobs are not done increase at an increasing rate with time spent foraging. Thus optimal time spent foraging should be given by the intersection of these two rate curves at T_{opt} where the net energy accrued is

$$\int_{0}^{T_{\text{opt}}} (dG/dT - dL/dT)dT \qquad (4)$$

where G is the energy gained and L is the energy lost. This model distinguishes between energy (intake) maximizers and time (spent) minimizers. The shapes of the gain and loss rate curves will determine optimal diet breadths.

I have devised another model (*25*) which has the advantages of (i) great generality, (ii) using the fitness of generalist (broad diet) or specialist (restricted diet) species as an optimality criterion, and (iii) encompassing, among other outcomes, the results of the models just mentioned. It has additional versatility because it describes the way in which fitness varies over a gradient of resource mixtures, and incorporates the effect of competitors. The model has three basic variables: resource similarity, resource productivity or density, and a parameter W_{min} which varies with the turnover rate of individuals in the population.

To demonstrate the use of this model, let us consider oak trees and pine trees to be two distinct resources. The two occur in mixed stands in many woodlands in the foothills of mountain ranges in the southwestern United States. Often the distribution of these trees is such that pure oak woodland occurs at the lowest elevations and pure ponderosa pine forest occurs at the highest elevations. Thus the proportion of oak trees present, p, decreases from 1 to 0 along an elevational gradient. Two warbler species may occur together in this woodland; they are similar in many ways except that one, the black-throated gray warbler *Dendroica nigrescens*, prefers oak trees, and the other, Grace's warbler *Dendroica graciae*, prefers pine trees (*26*). We can assign each species a fitness W in its preferred tree type, and a fitness qW in its nonpreferred type. The fraction q is therefore an index of resource similarity. Because this is an open woodland the birds must fly between trees spaced some distance apart. At a particular tree density a generalist species that finds all tree types acceptable may spend proportion k of its time traveling between trees and $(1-k)$ feeding in them. Therefore $(1-k)$ is an index of resource density. Note that a specialist that feeds only in oaks flies an expected distance $1/p$ where the trees are spaced at unit distances apart, and it will therefore spend proportion k/p of its time traveling and $(1-k/p)$ feeding in them.

Let us consider first the behavior of one warbler that has the woodland all to itself. If the black-throated gray warbler occurs alone in the woodland its fitness as an oak specialist is $W^{(1-k/p)}$; if it behaves as a generalist and visits both oaks and pines its fitness is a function of p,

$$W^{(1-k)p} \, (qW)^{(1-k)(1-p)} \qquad (5)$$

with components which reflect fitness in oaks and pines, respectively. The fitness of the specialist falls gradually at first but at an increasing rate as p decreases from unity, whereas the oak generalist fitness falls most rapidly at high p and at a decreasing rate with decreasing p (Fig. 3A). Thus the two curves intersect at some intermediate value of p, that is, at a critical value, p^*. At values of p above p^* the black-throated gray warbler should behave as an oak specialist and ignore the pines, but at values below p^* it should visit trees as they are encountered and act as a generalist. In sparser woodlands with higher k the switch from oak specialist to generalist along the gradient should be made sooner, at higher proportions of oaks, and as relative fitnesses in oaks and pines become more different (q decreases) the switch from specialist to generalist should be delayed until fewer oaks and more pines are encountered. Both lowered resource abundance and increased resource similarity favor a generalist over a specialist strategy.

Let us now consider the effects of adding another species, Grace's warbler, which is a pine specialist. The general result can be foreseen, in that the switch from oak specialist to generalist will be delayed in the presence of the pine specialist, and vice versa. Thus the competitor, by reducing the value of the nonpreferred resource, has the effect of decreasing q or decreasing k. Suppose the oak generalist feeds off the same tree as the pine specialist. When alone, the fitness of the oak generalist is as shown in Eq. 5, while the fitness of the pine specialist alone is

$$W^{\left(1-\frac{k}{1-p}\right)} \qquad (6)$$

Thus the total fitness derived from pines is

$$(qW)^{(1-k)(1-p)} + W^{[1-k/(1-p)]} \qquad (7)$$

and this fitness is shared proportionally by the two species when they occur together. Therefore coexistence between the pine specialist and the oak generalist will reduce fitness for the oak generalist to

$$\frac{q^{2(1-k)(1-p)}W^{(1-k)(2-p)}}{W^{[1-k/(1-p)]} + q^{(1-k)(1-p)}W^{(1-k)(1-p)}} \qquad (8)$$

and fitness for the pine specialist to

$$\frac{W^{2[1-k/(1-p)]}}{W^{[1-k/(1-p)]} + q^{(1-k)(1-p)}W^{(1-k)(1-p)}} \qquad (9)$$

Parallel expressions describe the way fitnesses are reduced when a pine generalist encounters an oak specialist. Oak and pine generalists will generally not occur together, but their fitnesses can be similarly calculated. Fitnesses when both species are specialists are, of course, unaffected by the presence of a second species. The relations between fitness and oak tree proportion are given in Fig. 3B which shows that whereas the black-throated gray warbler would have switched from oak specialist to oak generalist at a value of 0.32, in the presence of Grace's warbler the switch is delayed until p is 0.12; the same is true for Grace's warbler if p is the proportion of pines in the habitat.

The actual presence or absence of warblers at any point along the gradient is determined by whatever minimal fitness will ensure persistence there. Extremely low fitnesses would be ruled out if the individuals in question did not raise enough young or gain enough experience to offset the risks undertaken. If all fitnesses above some value $W_{\min}$ are permissible and worthwhile for the breeding individual, then the possible combinations of specialist or generalist black-throated gray warblers and Grace's warblers are as shown in Fig. 4, along with the mixes of oak and pine trees at which the changes should occur. For most values of $W_{\min}$ the pattern for warblers goes from oak specialist, to oak specialist plus pine specialist, to pine specialist, but if low fitnesses are permissible pine generalist and oak generalist, respectively, are added to the ends of the series to coexist with the other specialist. If only high fitnesses are permissible neither species may be present in the middle of the gradient, and a hiatus of ranges can result. Perhaps a third species with rather better fitnesses on the equal mixes of oaks and pines could invade successfully.

The following conclusions can be drawn from the model.

Resource abundance. High resource abundance or renewal rate (low k) favors specialists over generalists, and low resource abundance (high k) favors generalists.

Resource similarity. A mix of similar resources (high q value) favors generalists over specialists, and dissimilar resources support specialists.

Coexistence of exploiting species. The addition of a competitor effectively decreases q, and favors a wider range for specialists. There is a large range of environments over which specialists will coexist, a smaller range where a specialist will coexist with a generalist, but two generalists should not occur together. Further, when two species are available, a generalist will never occur alone, but will always coexist with a specialist.

Effect of population turnover rate. Where the premium on breeding, despite potentially low returns, is high (low $W_{\min}$), extended coexistence will be observed (*27*). This is equivalent to an r-selection situation, and produces overlapping ranges of species on the environmental gradient. Where high-risk breeding should be avoided (K-selection, high $W_{\min}$), coexistence over the gradient is decreased. Contiguous or abutting ranges, and even hiatuses in the combined ranges of species along the gradient, are to be expected (*28, 29*).

The optimal foraging strategies thus vary predictably with a few, relatively simple, environmental parameters. The predictions from this model are easily adapted to a variety of resource exploitation situations, and coincide with the predictions from other models, despite the range of model structures. For this reason, and because no more than simple logic and few assumptions were needed, they are likely to hold. Preliminary observations on the warbler species indicate that behavioral switches from specialist to generalist modes do occur within local populations, but more definitive data are required.

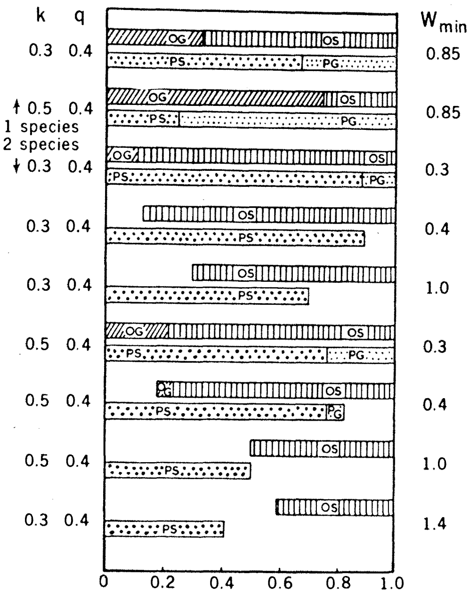

Fig. 4. Coexistence patterns for various values of resource similarity q, resource density k, and population turnover rates $W_{\min}$. Each of two species may occur or not, either as a specialist or as a generalist, over various parts of an environmental gradient going from proportion 1 of their preferred resource type to proportion 1 of their nonpreferred resource type. See text for further explanation.

Optimal Foraging Pathways

I shall conclude this article with a brief account of optimal solutions to yet another aspect of feeding ecology, that of how best to travel over a feeding area so that food intake is maximized. First one should note that most animals breed when food supplies are dense, and that dense food supplies can be defended. Thus most temperate land birds defend territories in the breeding season. The territories of such birds are usually less than a hectare in size, and any intrusion is easily spotted and repelled. But some species exploit food supplies which, even in the breeding season, are of such densities and distributions that the foraging individuals have to travel many kilometers to find food. In such cases food supplies cannot be defended. The food is exploited by individuals with overlapping ranges, foraging independently (for example, many seabirds) or grouped into flocks (for example, some North American blackbirds).

Many species that are territorial during the breeding season spend the winter in flocks. Most finches (families Emberizidae and Fringillidae) are good examples of this. Given that low food density prevents efficient defense of feeding sites, there are two questions to answer: Why are groups selected over individuals as the units of food exploitation, and how does that group

Table 2. Data from 14 flocks of birds in the Mohave Desert during spring 1968 (*30*). The symbols A, R, L, and B are for the direction ahead, right, left, and back, respectively (1 foot = 0.3 m).

Flock No.	Time observed (min)	Distance traveled (ft)	Average speed (ft/sec)	No. of species	No. of individuals	Distance from mountains (ft)	Path of flock: directional probabilities				Average straight (ft)	Seed density (g/m²)	Seed ripening rate*
							P(A)	*P*(R)	*P*(L)	*P*(B)			
4	105	1520	0.242	3	58	100	0.75	0.09	0.11	0.05	254	6.1	
1	120	1764	0.243	4	101	200	0.72	0.23	0.05	0.00	218		
3	115	2550	0.370	3	44	200	0.76	0.11	0.10	0.03	283	5.2	0.017
11	72	860	0.199	4	20	200	0.75	0.00	0.15	0.10	143		($N = 4$)
8	86	1494	0.289	4	164	800	0.71	0.11	0.18	0.00	136	1.3	
Averages			0.269	3.6	77	300	0.74	0.11	0.12	0.03	207	4.2	
14	120	2195	0.305	3	32	1050	0.75	0.08	0.15	0.02	161	1.0	
10	50	920	0.308	3	49	1200	0.70	0.10	0.20	0.00	205	0.9	
5	67	600	0.150	4	59	1500	0.72	0.28	0.00	0.00	200	1.3	
12	65	1392	0.356	3	49	1700	0.69	0.15	0.12	0.04	232	1.3	0.026
13	84	2010	0.399	3	115	1700	0.70	0.07	0.23	0.00	343		($N = 1$)
Averages			0.306	3.2	61	1430	0.71	0.14	0.14	0.01	229	1.0	
2	105	1725	0.274	4	88	2500	0.51	0.21	0.24	0.04	121	0.9	
6	87	2270	0.436	1	100	5000	0.76	0.18	0.05	0.01	239	0.4	
9	65	1540	0.395	4	49	5600	0.63	0.21	0.10	0.06	140	0.4	0.039
7	55	955	0.289	2	24	6900	0.41	0.29	0.20	0.10	74		($N = 5$)
Averages			0.365	2.7	75	5000	0.58	0.22	0.15	0.05	143	0.4	
First 7 flocks			0.280	3.4	67	536	0.73	0.10	0.14	0.03	200	2.1	0.018
Second 7 flocks			0.329	3.0	69	3557	0.62	0.20	0.14	0.04	164	0.5	0.033

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* The seed ripening rate is determined by field experiments that harvest ripe seeds daily from quadrats at different distances from the mountains.

move to optimize its foraging efficiency (if it does)? The answers to these two questions are connected in several ways.

I have looked closely at wintering finches in the Mohave Desert in southeastern California, particularly during March and April (*30*). Their food supply during these months consists of the seeds of annual plants, especially grasses, mustards, and storksbill, *Erodium*. About 80 percent of the food supply comes from storksbill, but in spite of this low resource diversity as many as a dozen finch species occur together and form large and complex mixed-species flocks. Such flocks have attracted a good deal of attention from a variety of biologists, and have elicited a variety of explanations: better defense against predators, easier formation of pairs or dominance-subordinance hierarchies, more efficient food exploitation.

It soon became clear that the Mohave Desert flocks are formed as a result of natural selection acting through the food supply. The birds appear to have no predators of consequence, some mated pairs forage preferentially with the flocks, and there is very little social behavior between individuals, especially between individuals of different species. Additional evidence for food supply being of prime importance comes from the finding of correlations between changing food supply and various aspects of the flocking phenomenon. Flock size, composition, and behavior vary predictably (i) between years of high and low food density, (ii) as the winter season progresses with ever-decreasing (nonrenewing) food supplies, and (iii) over a food density gradient that is higher at the wetter mountain base than it is in the desert plain. Flocks do not form at all when food densities are high, for example, during years of high rainfall when the amount of rain is one or two times the yearly average of 4.5 centimeters; but flocks become larger, more cohesive, and better organized with decreasing food supply.

From February to April, the latter half of the rainy season, the food supply changes from the previous year's leftover seeds to a new spring crop, with a peak in production around early April coinciding with the highest diversity and density of finches. At this time the resident and wintering birds are joined by large numbers of passage migrants. Why do they all feed together rather than independently?

I hypothesized that flocks act as "return time regulators." That is, a flock can move in such a way that (i) the variance of the time intervals between successive visits to a point in the habitat is minimized, and (ii) the mean return time interval can be adjusted such that in the interim food supplies have replenished to the extent that the site is worth revisiting. In this way the individuals of the flock are assured of feeding always on fruitful ground. But individuals that feed independently have no such assurance, and might waste a considerable portion of their foraging effort searching where others have recently fed and depleted the renewing food source.

Such a system will only work if flocks do not cross each other's paths; an early observation was the high consistency with which a flock of a given size and composition could be found in roughly the same location several days in a row, and so this requirement seems to be satisfied. Flocks appeared to have a foraging area of about 400 meters across, and to follow seemingly erratic paths which turned every 30 to 40 meters. To see how such a bounded area should best be traveled to maximize the uniformity of the coverage, William Rand of the Massachusetts Institute of Technology wrote a computer program in which a "flock" traveled over a bounded, square grid of side length 11 units and step length 1 unit. At each grid intersection the "flock" could choose to continue straight ahead with probability $P(A)$, to turn right or left with probability $P(R)$ or $P(L)$, or to reverse with probability $P(B)$. After 200 steps had been taken by the flock we examined how well it had covered the grid area for different sets of directional probabilities $P(A, R, L, B)$. As flocks in the field only rarely turn back on their tracks, we fixed $P(B)$ at 0.05. The results shown in Fig. 5 indicate that maximal coverage of 72 to 74 percent is obtained over a broad range of $P(A)$ values from 0.40 to 0.70, and from walks with a rather strong right- or left-handed skew or bias. Table 2 gives data on finch flocks, including their directional probabilities; it shows that all flocks move in such a way that return time variance is minimal.

How can flock behavior influence the mean return time, given that low variance is guaranteed? There are three variables which can affect the rate at which sites are revisited: flock speed, the distance between successive turns, and the set of directional probabilities. Because the flock is moving in a bounded area, mean return time will decrease as (i) flock speed increases, (ii) the probabilities deviate from $P(A)$ high, $P(R, L)$ low toward $P(A)$ low, $P(R, L)$ high. The flocks in Table 2 are listed according to the distance from the base of the mountains they were found feeding, that is, in order of feeding on decreasingly productive desert. The last two columns of the table show that, as one proceeds out from the base of the mountains, the food density decreases exponentially from more than 6 grams per square meter at the base to less than 0.5 g/m^2 1.6 km away from the base. High food densities are produced by more abundant moisture, which is supplemented by runoff near the mountains; the same factor, moisture, determines the rate at which the food is released, which is simply a desiccation process in these annuals. Thus ripening rates increase as food density decreases, as documented in the last column of the table.

One can therefore expect that flocks will return more quickly to points distant from the wetter mountain base, but must maintain longer return times close to the mountains. Table 2 shows that this is exactly what happens. In each of the three parameters that control mean return time, flock behavior varies with food renewal rate in exactly the way predicted for optimal return times. The variation is consistent in each of the three parameters: flock speed increases with distance out from mountains; distance between turns decreases with distance; and among directional probabilities $P(A)$ decreases with distance out from 0.74 and through 0.71 to 0.58, while $P(R)$ and $P(L)$ increase from 0.23 through 0.28 to 0.37. This amounts to a return time at 170 m out from the mountains (the average of the first seven flocks) twice as long as the return time at 1080 m (the average of the second seven flocks), and this difference in mean return time conforms well with food renewal rates that are almost twice as rapid out in the desert as close to the mountains. Finally, food intake, I, for these birds is proportional to the area searched (or flock velocity v), food density F, and food renewal rate $R : I \alpha vFR$. Variations in flock behavior, therefore, tend to keep the birds equally well fed over the variable food gradient.

Although more data are needed on finch flocks, these studies enable one to recognize and identify solutions to several optimization problems. Further studies should bring to light many more, and eventually we will know enough about local optima to understand the elegant and complicated compromises between them that obscure much of ecology.

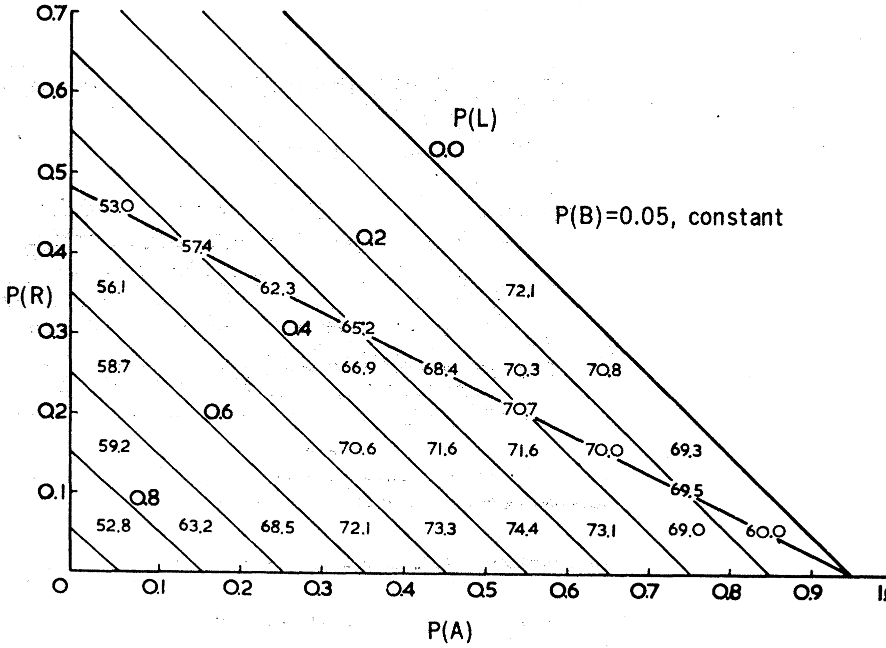

Fig. 5. In a bounded random walk the probabilities of a "flock" moving ahead, right, left, or back are expressed as $P(A)$, $P(R)$, $P(L)$, and $P(B)$, respectively. For various sets of these directional probabilities the figures show what percentage of a grid measuring 11 by 11 units is covered by the flock in 200 steps. [From (*30*); courtesy of Academic Press, New York]

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$$(k/\pi)\,AF\,(p-t) = kr^2F\,(p-k'r/\sqrt{2})$$

where k and k' are constants of proportionality, $A = \pi r^2$ is territory area, F is food density, p is the proportion of budget that goes for feeding the young, and t is traveling time. When the species become interspecifically territorial, N_2 is given by $kr^2F(1+\alpha)(p-k'r/2)/2$. Thus interspecific territoriality is profitable when $N_2/N_1 > 1$, or when $1 < [K-(r/2)]\,(1+\alpha)/2[K-(r/\sqrt{2})]$, where K is p/k'.

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Should the History of Science Be Rated X?

The way scientists behave (according to historians) might not be a good model for students.

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An editorial in the Washington *Post*, bemoaning double-talk from both sides during the last presidential election campaign, suggested that public reporting of the campaign, being harmful to the ideals of young readers, might be a proper target for censorship (*1*):

> It is time to consider whether this campaign ought not to be rated X for children, on the grounds that young and inexperienced minds might form the impression that our national politics is mainly composed of hypocrisy and cynicism. Adults know that to be wrong, of course, but there is not much in the current campaign by which to prove it.

Such proposals are equally appropriate to a variety of subjects similarly remote from the realm of sex, which the term "X-rated" connotes (*2*). My concern in this article is with the possible dangers of using the history of science in science education. I will examine arguments that young and impressionable students at the start of a scientific career should be shielded from the writings of contemporary science historians for reasons similar to the one mentioned above—namely, that these writings do violence to the professional ideal and public image of scientists as rational, open-minded investigators, proceeding methodically, grounded incontrovertibly in the outcome of controlled experiments, and seeking objectively for the truth, let the chips fall where they may (*3*).

As is customary, "science" will be identified primarily with physics and early astronomy; these subjects usually furnish the successful examples of the scientific approach to be emulated in other fields.

The Conventional Description of Scientific Behavior

The introduction of historical materials into science courses is often motivated by the desire to give the future scientist not only facts and technical skills, but also the correct attitude or general methodology. His teachers want him to respect the standards of impartiality, logical rigor, and experimental verification of hypotheses and to refrain from excessive theorizing about new or unexplained phenomena on the basis of metaphysical, mystical, or theological preconceptions. As the philosophers of science put it, he should be able to distinguish between the "context of discovery" and the "context of justification"—scientific hypotheses may come in an undisciplined way from the creative mind, but they must ultimately face the test of comparison with experiment and observation (*4*).

Science textbooks generally place a strong emphasis on the experimental character of science. As Charles Kittel and his colleagues say in *The Berkeley Physics Course* (*5*, p. 4):

> Through experimental science we have been able to learn all these facts about the natural world, triumphing over darkness and ignorance to classify the stars and to estimate their masses, composition, distances, and velocities; to classify living species and to unravel their genetic relations. . . . These great accomplishments of experimental science were achieved by men of many types. . . . Most of these men had in common only a few things: they were honest and actually made the observations they recorded, and they published the results of their work in a form permitting others to duplicate the experiment or observation.

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