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Behavior, Energy and Fitness[1]

STEVAN J. ARNOLD

Department of Ecology and Evolution, University of Chicago,
Chicago, Illinois 60637

SYNOPSIS. Fitness relations in behavioral energetics can be studied using the optimality approach (cost-benefit analysis), correlational analysis of selection, the experimental approach and the comparative method, as well as other approaches. These approaches ask different questions, have different virtues and different deficiencies. By using the approaches in combination we could gain new understanding of the relationships between behavior, energy and fitness.

INTRODUCTION

My goal in this paper is to discuss the complementarity of some of the approaches used to study behavioral energetics. In particular I will focus on four approaches (the optimality approach, correlational analysis of selection, the experimental approach and the comparative method) that have been used (or could be used) to study the relationships between behavior, energy and fitness. These approaches should be seen as complementary rather than as competing. Often, however, these four techniques have been used singly and by different sets of researchers. Methodological isolation can cause us to exaggerate the virtues of our favorite technique and gloss over its limitations. I try to squarely face the deficiencies of four approaches and discuss how they can be remedied by using the approaches in combination.

A major focus will be on the connections between the optimality approach and correlational analysis of selection. The optimality approach is at the center of a continuing controversy (Lewontin, 1978; Maynard Smith, 1978; Gould and Lewontin, 1979; Lande, 1982; Krebs and McCleery, 1984). Practitioners of the cost-benefit or optimality approach inadvertently fan the fires of controversy by opening their papers with the assertion that "natural selection maximizes fitness." This innocent-sounding phrase is nonsense to evolutionary theorists, for, despite many decades of work, no one has discovered a fitness currency that is invariably maximized during evolution (Wright, 1969; Lewontin; 1978). In fact, however, this maximization principle is not crucial to the conduct of cost-benefit analysis. If cost-benefit analysis is pursued as an exercise in making predictions about selection, rather than evolution, it can be noncontroversial. The most original part of this paper is mapping between cost-benefit analysis and the statistical study of selection.

I do not attempt an exhaustive inventory of approaches to behavioral energetics. For example, I do not discuss the use of physical models of the organism, which can be extremely valuable in studying temperature relations (*e.g.*, Kingsolver and Moffat, 1982). Nor do I discuss biophysical models that can be used to evaluate the potential of the environment in permitting activity or energy gain (Porter *et al.*, 1973; Porter and Tracy, 1983). Endler (1986) discusses additional techniques for studying selection (*e.g.*, perturbation experiments) and stresses the value of using combinations of approaches.

OPTIMALITY APPROACH

The focus in using the optimality approach is to determine how the organism should behave in order to maximize rate of energy gain or some other currency (Pyke *et al.*, 1977; Krebs and McCleery, 1984). The goal of the exercise is to make predictions about behavior on the supposition of optimization. The problem, as Schoener (1971) pointed out, has three aspects: (1) choosing the currency to be optimized, (2) choosing appropriate cost-

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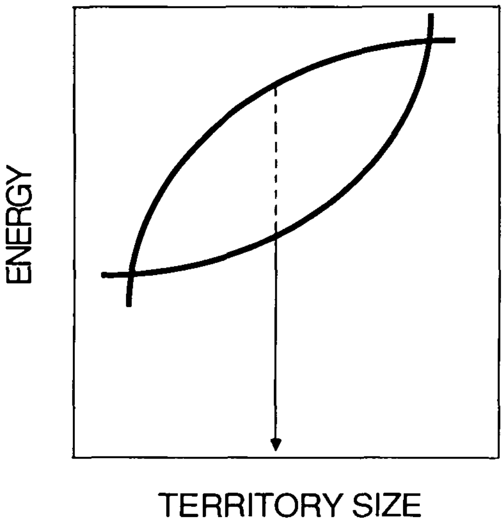

FIG. 1. A cost-benefit analysis of territory size. The benefits (in positive energy units) of holding a territory of various sizes are indicated by the upper, heavy line. The costs (in negative energy units) are indicated by the lower, heavy line. The dotted line indicates the territory size that yields the maximum net benefits.

benefit functions that specify the relationship between behavior and the currency and (3) solving for the optimal behavior. The success of the approach depends on whether the currency and cost-benefit functions are appropriate to the biology of the study species and whether the supposition of optimization is warranted. An example may make these points clearer.

Several authors have treated adjustment of territory size as an optimization problem (*e.g.*, Kodrick-Brown and Brown, 1978; Myers *et al.*, 1981; Hixon *et al.*, 1983; Davies and Houston, 1984). Following Brown's (1969) insight, these authors have viewed territory size as an economic problem. A territory of a particular size may yield benefits in terms of foraging success, but it may also incur certain costs for the owner who must patrol it. If both the benefits and the cost can be expressed in the same currency, then we can simply subtract the costs from the benefits to evaluate the worth or net benefit gained from a particular territory. One version of the argument is shown in Figure 1 for a continuum of territory sizes. Here we imagine that costs and benefits are evaluated in a common energetic currency. We further imagine that the energetic benefits level off with increasing territory size because, for example, there is a limit to how much food the territory owner can process. Costs, on the other hand, go up steadily with territory size, because more energy is spent patrolling and defending a larger territory. The rate of cost increase might go up continually (as shown in Fig. 1) or the cost function might be a straight line. In either case there will be an optimal territory size that yields the largest net energy gain. That optimal territory is easily found by locating the point on the x-axis corresponding to the greatest distance between the benefit and cost functions.

The optimality approach is usually used to make rough, qualitative predictions rather than precise quantitative predictions. If we wanted to use Figure 1 to predict optimal territory size in a particular species, we would need to actually measure the cost-benefit function (a problem considered in the next section), for the optimal territory size critically depends on the shapes and location of those two functions. On the other hand, we can make qualitative predictions about how optimal territory size will change as a consequence of separate effects on the cost or benefit functions. For example, consider Kodrick-Brown and Brown's (1973) analysis for how hummingbird territory size should be affected by the density of flowers that are used as an energy source. Consider a cost-benefit analysis of the number of flowers that are defended in the territory (rather than territory size) and assume that the benefit function is concave downward and the cost function is concave upward, as in the preceding example (Fig. 2). Imagine two hypothetical birds with the same number of flowers in their territories. In one bird's territory the flowers are spread over a large area, and consequently the territory is costly to defend. In the other bird's territory the flowers are dense and occupy a small area, so the territory is less costly to defend. This contrast in costs corresponds to a vertical line drawn anywhere on the left side of Figure 2 that intersects the two

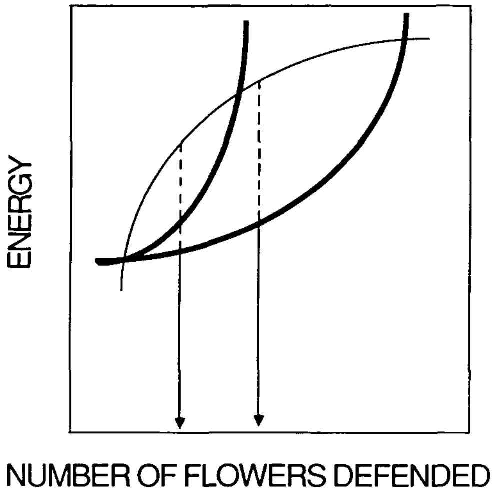

FIG. 2. Using an optimality argument to make a prediction. When flowers are dense (heavy line to left), the cost of defending a given number of flowers is less than when flowers are sparsely distributed (heavy line to right) and a larger area must be patrolled. When flowers are dense, the optimal territory should contain fewer flowers (after Kodrick-Brown and Brown, 1978).

indicated cost functions. In an environment with flowers at high density, a particular number of flowers is less costly to defend than in an environment of low flower density, because the flowers occupy a smaller area. The benefit functions are identical in the two environments, however, because the same energy is gained from a particular number of flowers, whether they are densely or sparsely distributed.

Kodrick-Brown and Brown (1978) used such an analysis to predict how territory size would vary with flower density. According to the analysis, when flowers are more dense, hummingbirds should defend smaller territories. The prediction was borne out in a field study of hummingbird (*Selasphorus rufus*) territories. The birds were migrants that maintained their territories for only a few days at a stop-over point in northern Arizona.

Virtues and limitations

The primary virtues of the optimality or cost-benefit approach are that it is easy to use and it produces testable predictions.

The main limitation of the approach is that its predictions rest on an optimization principle that is usually untested. This dependency is examined in detail in the next section. A further, unsatisfying aspect of many applications of the cost-benefit approach is that variation within populations is ignored.

The deficiencies of the cost-benefit approach can be remedied by using it in combination with other approaches. While most cost-benefit work has not focused on testing critical assumptions, those assumptions can be identified and tested using correlational studies of selection (next section). Comparative studies have more often been used as a companion in order to test the predictions of the cost-benefit analysis. However, while comparative work might be used to confirm predictions, the predictions themselves can be tested more directly with experiments or correlational studies of selection.

CORRELATIONAL ANALYSIS OF SELECTION

The primary question addressed by this methodology is, "How does contemporary selection act on the population?" The aim is to characterize the action of natural selection within generations. The aim can be achieved by describing the statistical relationship between phenotypic traits and fitness using the natural variation that occurs within populations (Arnold, 1983; Lande and Arnold, 1983; Arnold and Wade, 1984*a*, *b*; Manly, 1985; Endler, 1986).

Behavior, energy and fitness

To apply the method to a study of behavioral energetics, one would want, in the ideal case, data on behavioral traits (*e.g.*, display rates, average foraging rate, etc.), energy balance (*e.g.*, rate of energy input, average level of energy reserves, etc.), and lifetime fitness (*e.g.*, number of progeny) for each individual in a large sample. For example, Carpenter *et al.* (1983) show how the rates of energy gain of individual hummingbirds (*Selasphorus rufus*) can be measured in the field. The energetic traits should be appropriate to the ecology of the

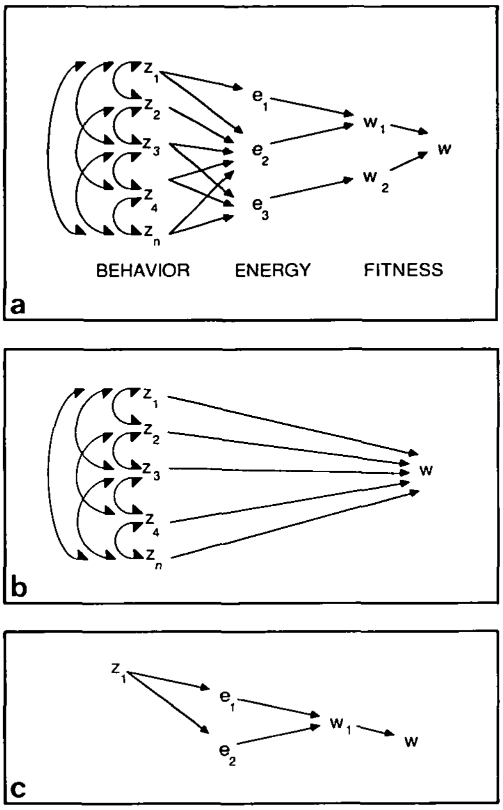

FIG. 3. Selection gradients and energy gradients. (a) The statistical relationships between behavioral variables (z_1, z_2, . . . , z_n), variables describing the energy balance (e_1, e_2, e_3), fitness components (w_1 and w_2, representing survivorship and fecundity) and lifetime total fitness (w) can be represented by a path diagram, as in this hypothetical example. Direct causal paths are represented with single-headed arrows. (b) Selection gradients for the behaviors are direct paths to fitness in this simplified version of Figure 3a. (c) The selection gradient for behavior z_1 is composed of two paths through two different energy variables. The first portion of each of these paths is an energy gradient.

study species and should capture the spirit of prevailing ecological attitudes as well as alternative hypotheses. Thus if the study species was thought to be an energy maximizer, we might measure rate of energy gain on each individual, but we might also measure time spent foraging so that we could test the alternative hypothesis of time-minimization.

The multivariate version of the problem is shown in Figure 3. Figure 3a is a path diagram in which the single-headed arrows represent the direct effect of one variable (at the beginning of an arrow) on another variable (at the end of the arrow). These single-headed arrows represent partial regression coefficients; double-headed arrows represent correlations between variables. A path diagram, such as Figure 3a, can be used to represent a series of multiple regression equations describing the statistical dependency of energy variables on behavior, as well as the dependency of fitness on energy or on behavior (Wright, 1921, 1934, 1968; Li, 1975). The figure shows the special case in which all of the effects of behavior on fitness are mediated through effects on energy balance.

Selection gradients and energy gradients

The coefficients represented by the paths in Figure 3a also play an important role in evolutionary theory. Consider the simplified diagram shown in Figure 3b in which we have eliminated the energetic variables and fitness components that intervene between behavior and fitness. The paths shown as direct arrows from behavior to fitness are known as *selection gradients* (Arnold, 1983; Lande and Arnold, 1983). The uppermost arrow, for example, is the selection gradient for the first behavioral trait, z_1. It is the coefficient of partial regression of fitness on z_1, holding all other behavioral traits constant. This coefficient represents the direct force of selection on z_1 holding constant effects of selection acting through correlated characters. Selection gradients, in conjunction with quantitative genetic measures of inheritance (genetic variances and covariances), can be used to predict the evolutionary response to directional selection (Lande, 1979).

The selection gradient for a particular behavior is composed of (1) effects of behavior on energy and (2) effects of energy on fitness. We can see the composition of the selection gradient for behavior z_1 by returning to Figure 3a and isolating those paths that constitute its selection gradient (Fig. 3c). Using a basic theorem of path analysis, we can show that the selection gradient for z_1 is the sum of two paths: one that passes through e_1, and one that passes through e_2. The two paths share a common element from w_1 to w. For convenience, we will call the initial portion of each path an *energy gradient.* It describes the effects of a particular behavior on an energy variable, holding constant other behavioral variables. Thus the selection gradient for a given behavior can be represented as a series of paths and each of these is composed of an energy gradient and a selection gradient for a particular energy variable.

Time scale and the effects of energy balance on behavior

In seeking the relationship between cost-benefit analysis and effects on fitness, time scale is of critical importance. The most appropriate currency for measuring total selection on behavior or energetic variables is total fitness measured as lifetime production of offspring. In order to measure selection on behavior, we are concerned with individual differences and wish to compute the statistical relationship between lifetime fitness and behavior averaged over the lifespan or over large intervals of the lifespan (*e.g.*, juvenile territory size, foraging success as a third-year adult, etc.). In contrast, cost-benefit analyses in behavioral ecology or behavioral energetics are commonly pursued on much shorter time scales. In the following discussions I have in mind studies of behavior, energy and fitness that measure these variables over whole lifespans, or major parts of the lifecycle, so that individual differences can be characterized.

On a short time scale, lasting a small fraction of the lifespan, Figure 3 might be a gross simplification. Energy balance might feed back on behavior, for example: stressed animals might forage less or curtail reproductive behavior. Effects flow only from behavior to energy in Figure 3, but on a lifetime time scale this might not be a bad approximation. Also, our behavioral variables could include capacity to modify behavior in response to energy balance. In particular cases, however, it seems possible that unidirectional effects between behavior and energy might not be justified even after adopting a lifespan time scale. In such cases one might need a more complicated path diagram to capture the causal effects.

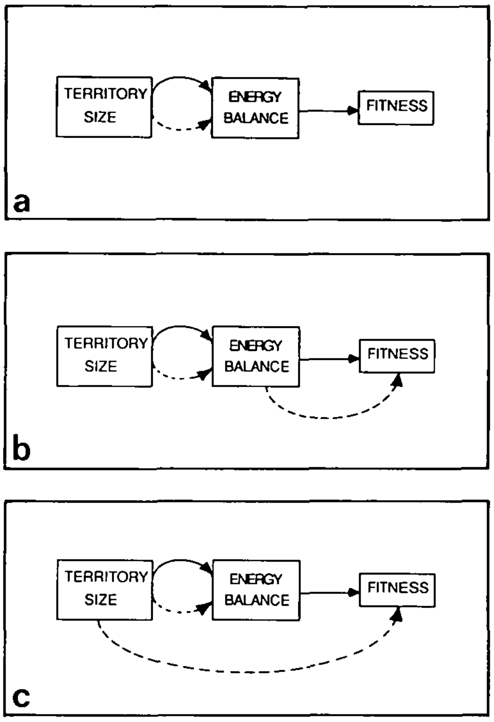

FIG. 4. All effects of behavior on fitness may or may not be mediated through the energy balance. (a) The case in which all effects of territory size are funneled through the energy balance. Solid arrows indicate positive effects (benefits), the dashed arrow indicates negative effects (costs). (b) The case in which the energy balance has both positive and negative effects on fitness. (c) The case in which some effects of territory size are mediated through the energy balance but there are also other effects on fitness.

Relationship between the energy gradient and cost-benefit curves

Energy gradients are equivalent to the average slopes of cost-benefit curves. In order to see this connection let us return to the earlier example of costs and benefits of territory size. Expressing the earlier logic as a path diagram (Fig. 4a), we imagine that larger territories give greater yields from foraging (solid arrow) but require more energy to patrol and defend (dashed arrow).

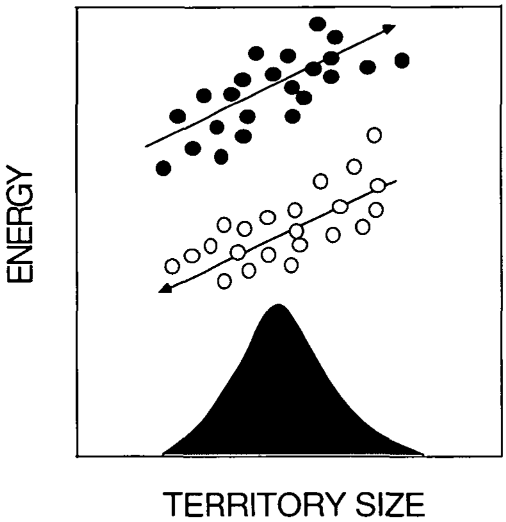

FIG. 5. Hypothetical data showing the estimation of energy benefit and energy cost gradients. The frequency distribution of territory sizes in the population is shown by the bell-shaped curve. Solid circles represent the average energy gains of individuals with different territory sizes. The slope of the line fitted to those points estimates the energy benefit gradient. Open circles represent the average energy costs to individuals with various sizes of territory. The slope of the line fitted to those points estimates the energy cost gradient.

We could estimate these benefits and costs directly if we had data on average energy gain from foraging, average energy expenditure for territorial defense and territory size for a large series of individuals. We could then plot the data, as shown in the hypothetical example (Fig. 5). We could also compute the ordinary least squares regression lines for the benefit and cost variables as functions of territory size (Fig. 5). These regression coefficients would be our estimates of the *energy benefit gradients* and *energy cost gradients.*

The relationship of these energy gradients to cost-benefit curves can be seen by superimposing the cost-benefit curves (which we will take as a given, for the moment) on the data plots (Fig. 6). We can see that the distribution of territory sizes in the population spans the middle portion of the benefit curve. At any point along the distribution we could draw a vertical line to the benefit curve and then draw a line tangent to the curve at that point. The

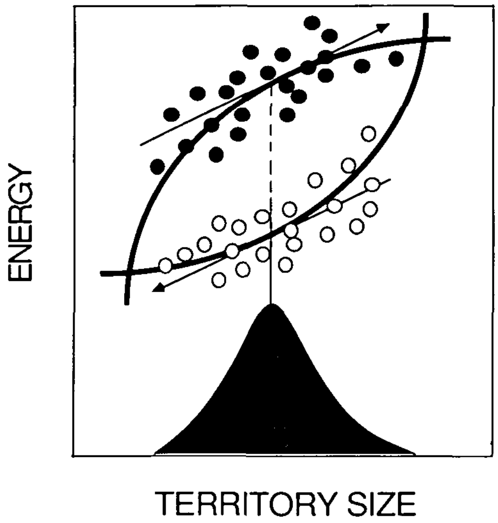

FIG. 6. Energy gradients superimposed on cost-benefit curves. The energy gradients are the average slopes of the cost-benefit curves, taking the average over the distribution of territory sizes. Conventions as in Figure 4.

energy benefit gradient is the average of these tangents or slopes. The average is taken over the distribution of territory sizes, weighting the slope corresponding to each territory size in proportion to the number of individuals with that territory size (*cf.* Lande and Arnold, 1983, eq. 9). Likewise the energy cost gradient is the average slope of the cost curve.

The cost-benefit argument that net benefit should be maximized can be recast in terms of energy gradients. In Figure 6 the territory size which gives maximum energy gain is indicated by the vertical line. At that territory size benefit minus cost is a maximum. That point also corresponds to a point of cancellation of the energy gradients. At the indicated territory size the benefit gradient is equal to the cost gradient but opposite in sign, so that the sum of the two gradients is zero. In other words, at the indicated average territory size there is no directional force of selection on territory size that acts via net energy gain.

The energy gradients will not cancel when the average territory size does not lie at the point of maximum net gain, and so territory size will experience a force of directional selection. Consider the case in

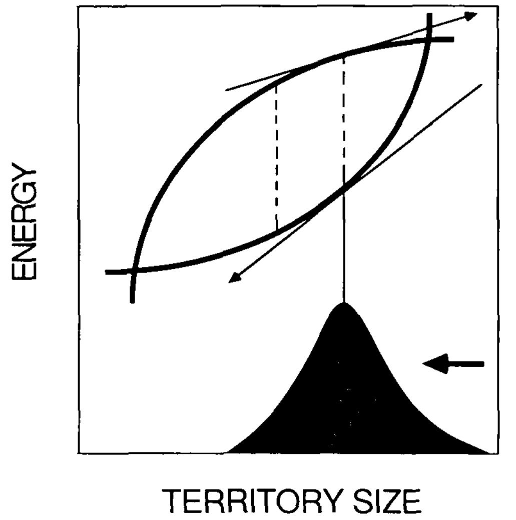

FIG. 7 Selection acting through the energy budget favors smaller territory size in the population when the energy cost gradient (slope of lower arrow) exceeds the energy benefit gradient (slope of upper arrow).

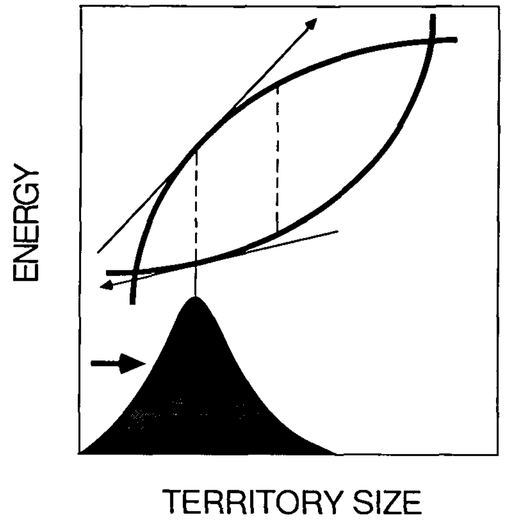

FIG. 8. Selection acting through the energy budget favors larger territories when the energy gradient (slope of upper arrow) exceeds the energy cost gradient (slope of the lower arrow).

which average territory size is larger than the optimum. The cost gradient will exceed the benefit gradient (comparing absolute values), which is equivalent to a selective force favoring smaller territories (Fig. 7). Likewise, when the average territory size is smaller than the optimum, the magnitude of the benefit gradient will exceed the magnitude of the cost gradient, and so a selective force favors larger territories (Fig. 8).

By combining the optimality approach with correlational analysis we can capitalize on the strengths of each approach. The cost-benefit curves are an excellent way to visualize conflicts inherent in energy demanding processes. Correlational analysis can allow us to measure the curves and explore their evolutionary consequences. In the preceding discussion we used the equivalence of the energy gradient with the average slope of the benefit (or cost) curve to rephrase the optimality condition (Fig. 6). We estimated the average slope of the benefit curve by computing the linear regression of energy input on territory size. Analogously, we could estimate the average curvature of the benefit curve by computing the curvilinear regression of energy input on territory size (*cf.* Lande and Arnold, 1983, eq. 14). Likewise the average curvature of the cost curve could be estimated by computing a curvilinear regression of energy expenditures on territory size. Cost-benefit curves need not be mental constructs divorced from ecological realities. Correlational analysis offers a way to estimate them directly from data and see whether actual curvatures fit *a priori* expectations. Correlational analysis can also enable us to see some of the critical assumptions implicit in evolutionary interpretations of cost-benefit analysis.

Critical assumptions in cost-benefit analysis

In order to make evolutionary predictions from cost-benefit curves we implicitly make some critical assumptions about fitness relationships. Consider the simple case in which these assumptions hold (Fig. 4a). We imagine that energy balance has a monotonic, positive relationship with fitness and that all effects of territory size on fitness are mediated through effects on energy balance. In this case, the path from energy balance to fitness (the energy balance selection gradient) is the final common pathway for selection acting via the costs and benefits of territory size. Because the energy balance selection gradient is the final common path, the population will achieve a selective equilibrium when the energy benefit gradient cancels the cost gradient (Fig. 6). It is possible, however, that even though the energy benefit and cost curves cancel, the population may not be at a selective equilibrium. In such cases the population may continue evolving and so depart from the outcome expected from a cost-benefit analysis that uses only an energy currency. An example of such a case is illustrated in Figure 4b. Here we imagine that a positive energy balance can be a liability as well as an asset. Thus when energy reserves are exceedingly high the animal may have difficulty locomoting and so may be more vulnerable to predation. In this case, the equilibration of average energy balance in the population may preclude equilibration of territory size. Schoener (1971) explicitly discussed the assumption that energetic currencies have a monotonic increasing effect on fitness, but the assumption has subsequently been taken for granted in the optimal foraging literature.

A second critical assumption needed to make evolutionary predictions from the cost-benefit curves is that all effects on fitness are mediated through energy currencies. Clearly this assumption may often be false. For example, the costs of defending a larger territory may include a greater risk of predation as well as bigger energy expenditure. In such cases, there are three paths from territory size to fitness, and directional selection vanishes when all three paths sum to zero (Fig. 4c). At selective equilibrium there might not be a cancellation of energy cost and benefit gradients if there is one or more non-energy paths to fitness. Because all effects of behavior on fitness are *not* funneled through the energy budget, treating energy as a "fitness surrogate" can give misleading results.

Evolutionary response to selection

The evolutionary response of the population to selection depends on aspects of inheritance. In order to visualize the effects of inheritance, consider first the simple case in which territory size is a genetically independent trait. Suppose, for example, that territory size is genetically independent of some other trait, such as body size. (We will soon define the concept of genetic coupling.) Genetically independent (uncoupled) traits are not affected by the evolution of other traits. The direction that such traits will evolve can be predicted solely from a knowledge of selection; genetic constraints can be disregarded. Figure 9 illustrates the case in which the environment has just changed, so that the population is no longer on an adaptive peak and, instead, selection favors a larger average territory size (but the same body size is favored in the new environment as was favored in the old environment). In this situation we can predict, using quantitative genetic theory (Lande, 1979, 1980) that the population will evolve directly towards the new adaptive peak. The picture dramatically changes if the two traits are genetically coupled. In this case the population evolves along a curved trajectory (Fig. 10a). Although the population begins at the optimal body size, the population evolves to ever larger, maladaptive body size. Finally the population slowly returns to smaller average body size as it approaches the optimum. The departure from optimum body size is due to genetic coupling or correlation.

Genetic coupling or correlation is revealed in the association between two traits in relatives (Falconer, 1981). Thus a genetic correlation between territory size and body size would be revealed in an association between the territory sizes of fathers and the body sizes of their sons (Fig. 10b). (Alternatively and equivalently, we could test for an association between body sizes of fathers and the territory sizes of sons.) To show that the association reflects genetic correlation, we would also need to show that the resemblance is not due to environmental effects (*e.g.*, by showing that cross-fostered sons resembled their real fathers more than their foster fathers). Genetic correlation is common among traits and can arise from pleiotropy. Thus the

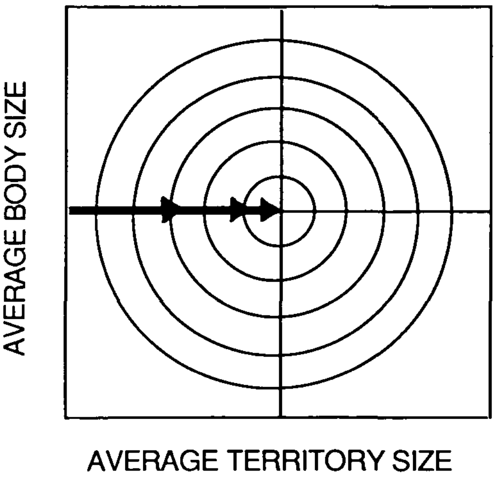

FIG. 9. Average body size and average territory size evolve directly to a new adaptive peak when the two traits are not genetically coupled. Concentric circles indicate fitness isoclines with a fitness peak at the center of the figure. If selection were frequency- or density-dependent, the population would evolve along a straight trajectory but would equilibrate downslope from the adaptive peak. The heavy line shows the evolutionary trajectory of the population. A constant number of generations has elapsed between successive arrow heads (after Lande, 1980).

same genes may influence both body size and territory size and so couple the two traits together. (Linkage disequilibrium is the other source of genetic correlation.)

Because evolution depends on both inheritance and selection, a correlational or cost-benefit analysis, which deals only with selection, yields only part of the information needed to make evolutionary predictions. A number of reactions are possible in the face of this *impasse.* (1) One could desist altogether from making evolutionary predictions from selection data. This is a highly defensible posture. Often times it does not represent any kind of retreat, for many ideas in behavioral ecology can be cast as hypotheses about selection rather than as predictions about evolution. (2) One can make qualified evolutionary predictions. This tack is tantamount to assuming no genetic constraints. (3) One could conduct a sensitivity analysis and determine whether reasonable values of genetic variances and covariances are likely to profoundly affect the conclusions. Finally, (4) one could combine measures of both genetic constraints and selection in making evolutionary predictions.

Besides inheritance, another problem in

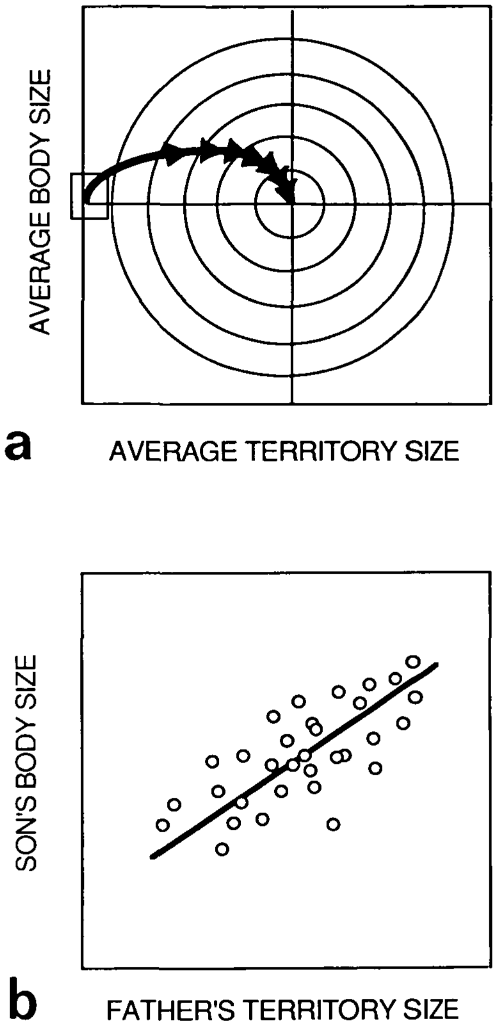

FIG. 10. (a) Average body size and average territory size evolve along a circuitous path to a new adaptive peak when the two traits are genetically coupled. If selection were frequency- or density-dependent, the population would evolve along a curved trajectory but would equilibrate downslope from the adaptive peak. (b) Hypothetical data illustrating the genetic coupling that causes the deflection of the trajectory. The deflecting effect can be visualized by focusing on the initial population surrounded by the small box at the left side of Figure 10a. Conventions as in Figure 9 (after Lande, 1980).

making evolutionary predictions from a data set that does not include measures of lifetime fitness is that the study of selection is incomplete. If we had data on behaviors, energy traits and lifetime fitness for a large series of individuals we could estimate the selection gradients for the behaviors and energy traits (diagrammed in Fig. 3). Combining those complete measures of selection with an inheritance study, we might be able to make rigorous evolutionary reconstructions and predictions. This goal has been achieved in some long-term studies (*e.g.*, Grant, 1986). However, although a study of energy gradients may not yield the complete resolution of lifetime selection needed to predict evolutionary response, it can test numerous hypotheses concerned with energy balance. The value of correlational analysis in this regard is that path diagrams can be used to see the relationship of the results to effects on fitness.

Virtues and limitations

The principal virtues of the correlational approach are that it can be used to measure actual selection pressures, the results can be directly mapped on formal evolutionary theory and it can be used to handle complex, multidimensional problems.

The main limitations of the approach are that it is labor intensive, sensitive to effects of unmeasured traits and it infers the target(s) of selection. The approach is labor intensive because it relies on statistical relations between data points based on individuals. The more individuals in the sample, the greater the statistical power to detect small effects. If, however, the individual attributes are difficult to measure (*e.g.*, average lifetime energy balance or lifetime fitness), application of the approach may be a huge undertaking.

Like all multivariate techniques, results can be affected by which variables are included in the analysis. Some aspect of territory quality, rather than territory size, may actually be responsible for the observed energy gradients (Fig. 5), for example. If we fail to measure that critical aspect of territory quality (correlated with territory size), we may wrongly conclude that territory size is *the* focus of territorial defense. While serious in principle, most researchers routinely cope with such confounding effects. Perhaps the best way to deal with the complication in the present context is to supplement the correlational analysis with an experiment that directly manipulates the putative target of selection.

EXPERIMENTAL APPROACH

The aim in using the experimental approach is to identify key variables that are capable of affecting behavior, energy balance or fitness. Putative causal factors are manipulated and effects on presumptive targets are monitored. With respect to fitness relations, the technique does not tell us whether selection actually prevails in the population. Instead we learn whether selection could act.

Supplementation and ablation are the basic categories of experimental manipulation. We can raise or lower the level of our presumed causal factors. For example, Ewald and Carpenter (1978) varied the level of food available to territorial hummingbirds (*Calypte anna*) in order to test the prediction that territorial behaviors would disappear both when food was scarce and when food was extremely abundant.

Virtues and limitations

The main virtue of the experimental approach is that it can give direct evidence for an effect on behavior, energy balance or fitness. Furthermore, it may be able to detect weak effects that would be difficult to document with the correlational approach. By extending the levels of a variable beyond the limits of natural variation the investigator may gain statistical power.

The experimental approach is not a panacea. Some traits are difficult or impossible to manipulate. Even when manipulation is possible, the consequences may vary according to the values of other uncontrolled variables. In such cases it may be necessary to use a series of multiple-trait manipulations. Finally, the technique does not tell us whether selection *is* acting; it only tells us whether selection *could* act.

The sign and the magnitude of the effect that is detected in the experiment can vary with the choice of experimental treatments. Consequently, we may conclude from our experiment that larger territories are beneficial, even though selection actually favors smaller territory size (Fig. 11).

THE COMPARATIVE METHOD

The primary goals of the comparative approach are to deduce phylogenetic relationships, identify traits that are prone to evolve and discover correlates of that evolution. The goal of phylogeny reconstruction is best pursued with multiple data sets and exhaustive sampling of relevant taxa. Because this is a major undertaking and so is usually pursued as a goal in itself, I will focus on the second and third goals. My focus is then on the student of behavioral energetics, pursuing comparative studies with taxa whose phylogenetic relationships have been deduced from independent data. By comparing taxa we can determine which traits have evolved, and by seeking correlates we can generate hypotheses about the selective forces responsible for that divergence (*e.g.*, McNab, 1980).

Clutton-Brock and Harvey (1984) give an excellent discussion of the comparative approach and its use in behavioral ecology. As they point out, comparative studies range from simple pair-wise comparisons of species, to comparisons of several closely-related species, to formal statistical analyses of species sampled from a diverse array of taxa. Each of these kinds of studies has its own advantages, but statistical treatment of multiple species can be used to disentangle effects that might confound interpretation of a simple contrast between two species. The confounding effects of body size, for example, can be controlled by using allometric relationships in comparative studies, as in the following example.

Both primates and carnivores show tremendous interspecific diversity in home range size (Harvey and Clutton-Brock, 1981; Gittleman and Harvey, 1982). In both taxa, average home range size varies over three orders of magnitude. Furthermore, home range size is related to metabolic needs (estimated from body size and the number of conspecific individuals that share a home range). The greater the metabolic needs of a group, the larger their home range. If we compare flesh-eating with insectivorous carnivores we find that the two groups have the same allometric slope, plotting log home range size against log metabolic needs, but the line for flesh-eaters has a higher elevation than the insectivore line (Gittleman and Harvey, 1982). Likewise in primates, the allometric relationship between home range size and metabolic needs varies with diet. Fruit-eating primates have proportionally larger home-ranges than foliage-eating primates, after we have accounted for differences in body size and metabolic needs (Harvey and Clutton-Brock, 1981). Thus comparative

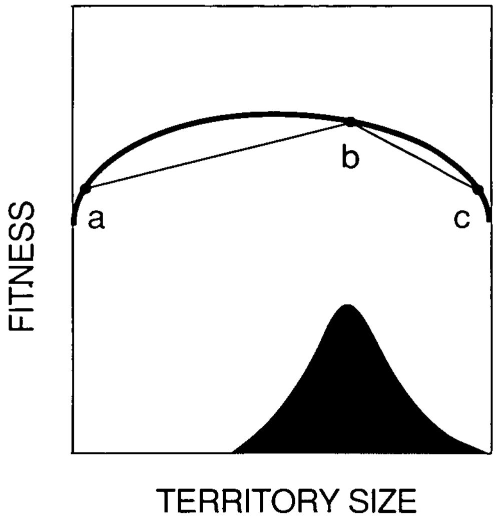

FIG. 11. The results of an experimental test for the fitness effects of territory size can depend on which treatments are contrasted. The actual prevailing relationship between fitness and territory size is shown with the heavy line in this hypothetical example. The frequency distribution of territory sizes is shown as the bell-shaped figure. If we contrast a territory size class much smaller than the average (a) with the average class (b), we could conclude that selection favors larger territories. If we contrast (a) with (c), we could conclude that no selection acts on territory size. A contrast between (b) and (c) could lead us to the correct conclusion that selection favors smaller territories. By contrasting only two territory size classes we could not detect stabilizing selection (curvature of the fitness function).

studies suggest that home range size coevolves with metabolic needs and that selection pressures vary with diet. These hypotheses about selection on home range size are compatible with intraspecific studies that show adjustment in home range size according to resource level (Gittleman and Harvey, 1982).

Statistical independence of taxa is an important consideration in using the comparative approach. If we use comparative data to show that larger species have larger territories, the relationship is compelling if all the species are distantly related; it may be a phylogenetic artifact if all the large species belong to one genus and all small species belong to another genus. Various methodological solutions have been proposed. One solution is to use genera or higher level taxa as data points, rather than species. Clutton-Brock and Harvey (1977) and Harvey and Mace (1982) discuss a formalization of this idea that uses nested analysis of variance. Classifications or, better, phylogenies can be used to estimate the minimum number of independent evolutions of a trait or trait environment combination (Gittleman, 1981; Lauder, 1981; Ridley, 1983). If a phylogeny is at least partly known, statistically independent contrasts between taxa can be abstracted from it (Felsenstein, 1985). Cheverud *et al.* (1985) present a methodology for separating phylogenetic effects and independent adaptation to different environments.

Virtues and limitations

A main virtue of the comparative approach is that it can suggest hypotheses about selection and adaptation (Clutton-Brock and Harvey, 1984). Resulting predictions may lack the conceptual clarity of predictions arising from the optimality approach, but they may have the advantage of being rooted in a broad taxonomic data base. Thus the comparative method can reveal associations that suggest widespread and recurrent themes of natural selection.

Predictions about selection gained from the comparative approach should be tested using the experimental approach or correlational analysis of selection. Associations identified with the comparative approach (1) may not represent causal relationships, (2) the explanation of the association may be wrong or (3) the direction of causality may be ambiguous (Clutton-Brock and Harvey, 1984).

CONCLUSIONS

(1) Different approaches used in studies of behavioral energetics have different strengths and weaknesses. (2) Often, when only one approach is used, limitations are ignored or glossed over. By using a combination of techniques, the limitations of one approach can be covered by a complementary approach. (3) The primary role of the optimality approach and the comparative method is to generate hypotheses about selection and adaptation. (4) Correlational analyses of selection and the experimental approach can be used to directly test predictions about selection. The two techniques are complementary. (5) The experimental approach can be used to test inferences about selection derived from correlational analysis. (6) Likewise, correlational analysis can complement experimental work by estimating the actual, prevailing selection pressures on a population. (7) Correlational analysis of selection can also be used to test the key assumptions used in optimality arguments.

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