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## VARIATION AND CHANGE IN BEHAVIORAL ECOLOGY<sup>1</sup>

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### INTRODUCTION

This paper argues for the importance of *time* in the behavioral ecology of changing environments; that is, how behavior changes in response to the time scale of environmental change. I distinguish between change, which occurs over time, and variation, which is measured instantaneously. Variation and change can be equated; this amounts to viewing a dynamical process as static. For example, a predator–prey oscillation involves changes, over time, in numbers of predators and prey. An atemporal measure of such changes might be the range of variation in population sizes, corresponding to the amplitude of the oscillation. Consideration of time scale tends to be submerged when variation is confounded with change.

There are two reasons why time-dependent behavior merits further attention. First, it has important ecological consequences. Second, in the theory of evolution in changing environments, questions of the time scales of phenotypic and environmental change are crucial. But such questions have received less attention in behavioral ecology. A further emphasis on temporal factors is needed to link empirical, behavioral studies of changing environments with theoretical, evolutionary ones.

After providing some definitions, to clarify what is meant here by time-dependent behavioral responses, variation, and change, I use some examples of the behavior of seed-eating ants to illustrate the ecological importance of time-dependent behavioral change. The following section reviews how current work on behavior in changing environments treats questions of variation and change, arguing that this work emphasizes instantaneous variation rather than temporal change. Finally, I consider how models of phenotypic response to changing environments, derived from other fields of evolutionary ecology, have explicitly considered temporal factors, and how these models might be extended to behavioral ecology.

Behavioral responses to environmental change can be of two kinds: those that depend on the time scale of environmental change, and those that do not. For example, an animal may be active at high temperatures, inactive at low ones. This behavioral response to an environmental condition is independent of time. But the amount of food the animal stores may depend on the rate at which temperatures change in the course of the autumn. Suppose food retrieval and storage are triggered by gradual changes of day length, temperature, and leaf cover. Then the animal may store less food when cold weather arrives very rapidly than when the weather slowly turns cold. In this example the behavioral response depends on the time scale of environmental change.

To distinguish between variation and change, let us define “variation” as differences among individuals at a given time, and “change” as differences in one individual as time goes on. For example, consider an ant colony as an individual organism. Harvester ant colonies forage for seeds along distinct trails. On a given day, one colony may use three foraging trails, another might use two, while a third might use four. These colonies vary in the number of trails they are using. From one day to the next, a colony uses different trails. Thus one colony may use three trails on day 1, two on day 2, and four on day 3. This colony is changing the number of foraging trails it is using.

“Behavioral change” will be used here to mean a change in the way that an organism performs a particular function. If the behavior is directed towards a particular goal, such as obtaining a certain amount of food, a change of behavior could entail a change in the manner of reaching the goal. A colony might obtain the same amount of food with few foragers on many trails, or many foragers on a few trails. A change of behavior could also entail a change of goal. On some days a colony does not forage at all, so no food is obtained. In addition, behavioral change can be reversible or irreversible. An irreversible change might occur if vegetation became so dense that trails were impossible to form. Reversible change, or behavioral flexibility, such as day-to-day fluctuations in the numbers of trails a colony uses, is the type of change most frequently considered in this paper.

<sup>1</sup> For reprints of this Special Feature, see footnote 1, page 1179.

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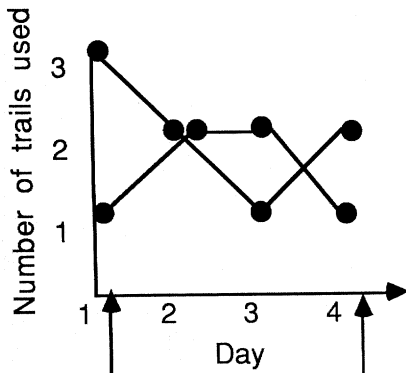


FIG. 1. Variation and change in trail use by ant colonies. The ordinate describes the magnitude of a behavior character, e.g., the number of foraging trails an ant colony uses on a given day. The abscissa represents time, here measured in days. Each curve shows the numbers of trails used by one colony, over a sequence of days. In the example described in the text, variation is measured at the times shown by arrows.

Change and variation are sometimes equated, because in a population change may lead to variation; that is, change can produce differences among individuals. But the relation of change and variation is not simple, because either can occur without the other (Lott 1984). When all individuals change in the same way, there will be change without variation. When individuals start out different and stay that way, there is variability without change. Moreover, when changes of individual phenotype lead to a similar outcome, these changes can be masked by a lack of variation among the individuals.

Fig. 1 illustrates one relation of variation and change. Suppose variation in the number of trails a colony uses is measured on days 1 and 4. The distance between curves, at the time that trail use in different colonies is compared, is a measure of the extent of variation. On day 4, variation will be less than on day 1. This is because of the way the magnitude of the behavioral character is changing over time. In general, when and how much individuals change will affect the extent of variation in a population.

#### VARIATION AND CHANGE IN THE FORAGING BEHAVIOR OF HARVESTER ANTS

An organism may respond only to the magnitude of environmental change; here the ecologically relevant consequence is variation, that is, diversity in the population. When the organism also responds to the temporal pattern of environmental change, then the dynamics of behavior, as well as variation in behavior, can be ecologically important. This section offers examples of how variation and change can each affect the ecology of an ant species.

In the desert of the southwestern United States, the red harvester ant (*Pogonomyrmex barbatus*) competes for limited seed resources with a guild of granivorous ants, birds, and rodents (Davidson 1985). A *P. barbatus* colony adjusts its foraging behavior to changes in its environment (Gordon 1991). A colony engages in various tasks outside the nest, including nest maintenance, patrolling (defense and scouting for food), midden work (sorting refuse), and foraging (retrieving food). Behavioral flexibility occurs at the individual level. Distinct groups of individuals tend to do specific tasks, but individuals switch tasks in response to changed conditions (Gordon 1989). To some extent, the causes of task switching are independent of time. For example, an ant from any other exterior task group will switch tasks to forage when an abundant food source appears. When there is extra nest maintenance work to do, no ants from other task groups will switch tasks to do it; instead, reserves are recruited from the pool of workers inside the nest.

Task switching leads to variation among colonies in the numbers foraging. Ants are channelled into foraging by the mechanisms that govern the direction of task switching. At any time different colonies, responding to these mechanisms from different starting conditions, will vary in the numbers available to forage. The amount of food retrieved by a colony is correlated with the number of ants working to collect it. Thus variation among colonies in forager numbers will influence the proportion of food resources obtained by each colony. The rule that says, "In the presence of abundant food, switch tasks to forage," leads to variation among colonies in behavior, and this variation can affect the foraging ecology of the species.

Task groups within colonies interact with each other (Gordon 1987). That is, the behavior of each group of workers is linked to that of other groups. This is a further source of variation among colonies. For example, the amount of foraging a colony does on a given day depends on events the same day that affect other task groups. If a colony is burdened with extra nest maintenance work early one morning, it will decrease the numbers foraging later on that day. Foragers become less active, tending to remain inside the nest, while more nest maintenance workers are recruited to do the extra work. Various kinds of events, such as flooding or windblown debris on the nest, affect the need for extra nest maintenance work. Such events will affect different colonies at different times. Foragers appear to act on a rule such as, "When the number of nest maintenance workers reaches a certain level, stay inside the nest." Both the requirement for nest maintenance, and the extent to which this requirement decreases the intensity of foraging, vary among colonies. This will lead to differences among colonies in the

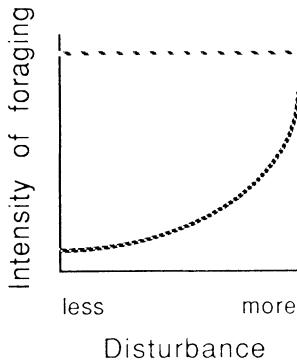


FIG. 2. Intensity of foraging in response to disturbance. The dotted line shows a baseline intensity of foraging in undisturbed *Pogonomyrmex barbatus* colonies. The curve illustrates the behavior of colonies exposed to environmental perturbation.

numbers foraging, which in turn affects the partitioning of food resources in the population.

Some interactions among worker groups are time dependent. A task group's response to a change of environment depends on how quickly the event occurs, and on how many other aspects of the environment are changing at the same time. In field experiments I introduced perturbations, each of which directly affected only the workers engaged in a single task. Combinations of different perturbations, performed simultaneously, had a synergistic effect. As the number of perturbations increased, the response of the colony tended to emphasize foraging.

For example, barriers on the foraging trails interfered with foragers, but no other worker groups encountered the barriers. The intensity of foraging in harvester ants decreases while a foraging trail is obstructed, before the ants can remove the barrier, or before foragers can be channelled to another trail. The numbers foraging also decrease when a sudden increase in the amount of nest maintenance work to be done requires new nest maintenance workers to be recruited from inside the nest. But if both perturbations occur at the same time, the numbers foraging decrease less. Thus the intensity of foraging depends on the temporal pattern of environmental change. The intensity of foraging seems to be regulated as shown in Fig. 2. The dotted line shows a baseline intensity of foraging in undisturbed colonies. The more that disturbances overlap in time, the more the numbers foraging approach those in undisturbed colonies. This gives priority to foraging at times when a widespread change of environment may also interfere with other activities, which may be less important.

This behavior depends on the time scale of environmental change because a disturbance is, by definition, a sudden departure from an expected or baseline condition. It involves a change of environment on a

shorter time scale than that of gradual, imperceptible adjustment. The magnitude of a disturbance depends both on how fast the change takes place, and on how fast the organism can respond. A power cut that occurs at night is a disturbance, because it is difficult to restore lights fast enough to carry on normal activity, but the onset of darkness that happens every evening is not a disturbance.

Interactions between species also involve behavioral response to the time course of environmental change. In some ways, it is *P. barbatus*' lack of response to change that makes it susceptible to interference by another seed-eating species of ant, *Novomessor* (= *Aphaenogaster*) *cockerelli* (Gordon 1988). *N. cockerelli* is active at night; *P. barbatus* is active from sunrise until about noon. *N. cockerelli* uses pebbles and bits of soil to plug the nest entrances of neighboring *P. barbatus* colonies early in the morning, before they emerge for the day. A plugged *P. barbatus* colony eventually digs its way out, but emerges about an hour late. The daily round of *P. barbatus*' activities outside the nest has a predictable sequence, and some aspects of the sequence do not change when a colony is disturbed. Patrolling, which includes scouting for new food sources, always occurs before foraging. This means that foraging always comes late in the activity period, even if the onset of activity is delayed by nest-plugging. The activity period ends when high soil temperatures force the ants back into the nest. When the activity period of a plugged nest begins late, foraging also begins late, and the time available for foraging is cut short by the afternoon heat. Food resources that might have been retrieved by a *P. barbatus* colony on the day it is plugged can still be available when the *N. cockerelli* colony emerges that night.

Nest-plugging would be ineffective if *P. barbatus* were more flexible, so that a plugged nest could begin foraging sooner after emergence, or would forage more in response to plugging. With regard to nest-plugging, the response of *P. barbatus* is like the flat line in Fig. 3: no matter what time foraging begins, the rate at which foragers leave the nest does not change. The environmental variable here is the time that foraging can start, which is affected by factors such as the weather and nest-plugging. To combat nest-plugging, a more effective response might be the one shown in Fig. 3 as a curve: foraging rates increase if the onset of foraging is delayed.

The response shown in Fig. 3 is time dependent. The environmental variable is the time of day at which conditions of light, temperature, and an unobstructed nest entrance make it possible for foraging to begin. This time-dependent environmental variable determines the behavioral one, the numbers foraging per day. Which species gets the seeds on a given day is

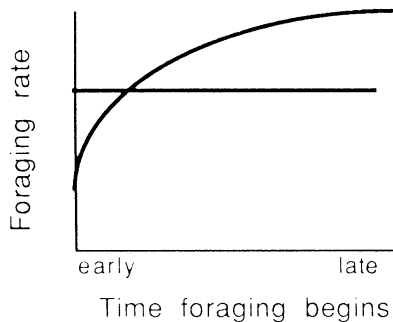


FIG. 3. Foraging rate as a function of the time that foraging begins. The ordinate represents the rate at which foragers leave the nest to search for food; the abscissa represents the time that morning that foraging began. The flat line corresponds to the observed behavior of *Pogonomyrmex barbatus*; the curve represents another, hypothetical strategy. The curve levels off to illustrate an upper bound on the number of available foragers in the colony.

affected by two kinds of temporal patterns. First, there is the pattern of interference, which includes when the nest is plugged, and when this occurs in the daily sequence of *Pogonomyrmex* activities. Second is the extent to which *Pogonomyrmex* responds to nest-plugging by foraging more, and by foraging earlier than in its usual sequence of activities.

The examples in this section show that an ant colony responds to changes of environment in many ways. Some of these responses depend on the time course of environmental change, while others do not. In both cases, behavioral change contributes to variation among colonies. To understand how such variation affects the foraging ecology of the species, it is necessary to consider the time scale of behavioral and environmental change.

#### VARIATION AND CHANGE IN BEHAVIORAL ECOLOGY

Though it may not always be presented this way, a huge body of work addresses the question of how behavior changes. Behavior is characteristic of a species, but also of types of individuals within species, such as individuals of a particular sex, age, or dominance status. With increasing detail, we have learned the rules specifying the conditions under which a particular type of individual will act in a particular way. Numerous studies show how environmental conditions, from temperature to the presence of certain conspecifics, can affect behavior. Behavioral flexibility is widespread and well documented (reviewed in Lott 1984, Caro and Bateson 1986, Wcislo 1989).

Amid all the work documenting behavioral change there is relatively little consideration of questions of time scale. This is not because behavioral ecologists have concluded that the time scale is unimportant in

the relation of behavior and environment. Instead, I think a reason for this lack can be found by examining the models usually employed in current research on this subject. The following is a very brief review of such models, in which I generalize and simplify in order to make a point: these models emphasize variation rather than change.

In behavioral ecology, behavioral change is one aspect of an area of research known as "alternative tactics." Several general questions are addressed: (1) The set of possible behavioral responses, real and imaginary, that might be appropriate to a particular situation, is sometimes called a "strategy set"; each response is a strategy. What behavioral strategies are possible, or plausible? (2) What are the developmental or physiological mechanisms of existing alternatives? (3) Under what conditions does a particular alternative enhance reproductive success? Research on alternative tactics is based on evolutionary questions. Much of this work draws on game theory and the idea of the evolutionarily stable strategy (ESS; Maynard Smith 1982). In game theory the problem is to discover which strategy will win. In ESS models the problem is to find the strategy that will persist in evolutionary time, conferring higher reproductive success than any other that may be introduced.

Behavioral alternatives can be evolutionarily stable when individuals practice a "mixed strategy." A mixed strategy implies variation in a population. It could come about in one of two ways. Either some individuals practice strategy A and others strategy B, or else individuals are capable of both A and B. The latter possibility requires individuals to change behavior, moving from one behavior to another at random. The former, which is sometimes called a "genetic polymorphism," only requires variation in behavior among fixed individuals. (Flexibility, when individuals behave differently depending on their assessment of changing conditions, would be a conditional strategy, not a mixed one.)

A mixed strategy can be an ESS when the advantages of each alternative, A or B, depend on the frequencies with which other players use strategy A or B. Parker (1974, 1978) used an ESS approach to predict how long male dungflies should wait on cowpats for prospective mates. For a given number of females, the benefit for a male of waiting on a cowpat depends on how many other competing males are present. Thus the optimal waiting time for a male depends on the frequency of other males. The number of males present on the cowpat will vary, as males fly on and off. This means the optimal waiting time of the remaining males will vary. In this situation a mixed strategy, composed of a variety of waiting times, is evolutionarily stable. Either every male has a fixed waiting time, and a variety of

males that differ in waiting times will exist in the population, or each male changes its waiting time.

Like Parker's, much research on alternative tactics seeks to determine an ESS in conditions of frequency dependence. Evolutionary dynamics depend only on the average numbers of individuals practicing strategy A and numbers practicing B (Zeeman 1981). Benefits are associated interchangeably with doing A sometimes or being an inflexible A type. This equates variation due to the presence of more than one type of fixed individual with variation due to individuals' changes of behavior. Thus evolutionary predictions about alternative tactics often do not distinguish change or transformation in behavior from intraspecific variation in behavior.

Behavioral variability may be related to environmental variability. One example of this is a frequency-dependent behavioral strategy: the optimal strategy for playing a game varies, depending on variation in the frequency of other types of players in the environment. Other models, especially in optimal foraging theory, consider in a more general way the fitness consequences of environmental variation. When the function of an animal's behavior is to obtain a resource, such as food or territory, success in acquiring the resource can be seen to add to the fitness of the animal by some increment called the "fitness value" of the resource. Variation in environmental conditions can cause the fitness value of a resource to vary. Caraco (1980) pointed out that, for example,  $N$  units of energy when an animal is near starvation may increase fitness more than  $N$  units when it is near satiation. (Phrased this way, it is the state of the animal, not the environment, that varies, but here variation in the animal's state can be taken to mirror variation in environment.) Caraco et al. (1990) studied how foraging juncos respond to situations in which environmental variation causes the fitness value of a food reward to vary. Enquist and Leimar (1987) incorporate variation in resource value into a game-theory model of fighting behavior. In their model, predictions of how long a fight will last, and who will win, depend on each participant's assessment of the current value of the resource they are fighting over.

Dynamic programming (Houston and MacNamara 1988) provides a general method for predicting optimal strategies in variable environments. Rewards obtained by means of various behavioral strategies, and thus the fitnesses associated with these strategies, are stochastic. That is, the fitness consequences of a particular behavior are defined by a probability distribution. A sequence of decisions is considered, and costs and benefits of a particular strategy are calculated in the context of the preceding decisions. Thus the optimal strategy depends on the sequence of decisions the animal makes. For example, small birds forage during the day and

must gain enough energy to ward off starvation at night. Choosing an alternative early in the day with low probability of energy gain may raise the cost of a similar, low-gain choice at dusk, when it is crucial to reach a threshold of energy reserves.

In general, research questions about behavior in heterogeneous environments are usually formulated as optimality problems. Behavioral response to environmental variability produces variant types, and the problem is to discover which type has highest fitness. This approach can be illustrated using an adaptive landscape to represent, not the relation of gene frequencies and fitness, but the relation of phenotype and fitness. The landscape is in a space whose axes represent the magnitudes of behavioral traits; a fitness value determines the height of each point. Asking why a strategy is optimal is asking why a peak is where it is; what are the environmental conditions that associate a high fitness with a particular behavior? For example, one environmental variable affecting fitness might be the frequency of conspecifics using a particular strategy.

The study of alternative tactics explores the possibility of  $> 1$  optimal behavioral phenotype. It supposes two peaks of similar height in a stable adaptive landscape, or a continuum of tactics, when the adaptive landscape contains a long ridge (e.g., Field 1989). The question is, Why is behavior A favored in condition  $x$ , and behavior B favored in condition  $y$ ? In optimal foraging theory, risk sensitivity and risk aversion are responses to environmental variability. The fitness of each type of behavior depends on the degree of heterogeneity present in the environment. The adaptive landscape itself does not change. Dynamic programming introduces the possibility of variation in behavior. The animal moves around on a fixed adaptive landscape, as it chooses among different types of behavior, such as ways to forage, and each choice of behavior entails a characteristic amount of resource or fitness obtained. The topography may include dangerous cliffs; for example, behavior of very low fitness might cause a bird to starve overnight. To specify an optimal strategy, dynamic programming takes into account the sequence in which an animal moves through an unchanging adaptive landscape.

The examples described above, models of behavioral responses to heterogeneous environments, all imply a stable adaptive landscape. Using these models, it is difficult to consider environmental change and the time scale of behavioral responses to it. Because fitness is a measure of a relation between phenotype and environment, adaptive landscapes are clearly not stable when conditions change; on the contrary, the landscape "undulates" in a changing environment (Kauffman and Levin 1987). Optimality and ESS arguments tend to be concerned with the search for equilibria, rather than

with change. Such arguments are more easily applied to measures of variation, which collapse the process of change into a single, instantaneous quantity, than to the transformation of behavior over time. This may be why behavioral ecology has been more concerned with static measures of heterogeneity than with dynamic measures of change.

#### THE EVOLUTION OF BEHAVIOR IN CHANGING ENVIRONMENTS

In behavioral ecology, hypotheses about the evolution of behavior in heterogeneous environments have emphasized variation, not change. But outside of behavioral ecology, models of evolution in changing environments have always highlighted the importance of time scale. Levins' (1968) models were set up in terms of the interplay between the "grain" of an environment, how fast it changes in time and space, and the dynamics of an organism's response. Such dynamics include how fast or slowly the phenotype changes, what lags exist between a stimulus to change and the response, how one kind of change affects another, and so on. Like any phenotypic response to environmental change, behavioral responses are affected by the sequence in which events occur, and their frequency. Slobodkin and Rapoport (1974) show that a type of irreversible behavioral change, learning, provides many examples of this. If the same perturbation recurs frequently and recognizably in an animal's lifetime, it may eventually learn a response that is different from its initial one. The temporal pattern of environmental change determines the organism's response to simultaneous events; it may have to decide to ignore some events and respond to others. The apparent frequency of a perturbation, from an organism's perspective, may depend on the time lag of the organism's response. Perturbations may occur so rapidly, relative to the organism's response, that it must respond to the average value of the oscillating environment rather than reacting to each stage of the fluctuation.

For the behavioral ecologist the salient questions about behavioral change are: (1) Under what conditions does change lead to intraspecific variation? (2) On what time scales do behavior and environment interact? (3) How do these dynamics affect reproductive success? To answer the first two questions, empirical work is needed. To answer the third one we need theories that connect behavioral change and fitness. This suggests an adaptive landscape with axes representing environmental variables as well as phenotypic ones. It associates fitness, as a height, with the set of all possible responses to environmental change. For example, consider the intensity of foraging behavior of harvester ants. The corresponding adaptive landscape includes both phenotypic and environmental

variables, and represents all possible foraging intensities in all possible environmental conditions. One relevant environmental variable might be temperature, and a line in the landscape describes how foraging intensity changes when temperature rises. The height of each point on the line associates a fitness value with this response. Decreased foraging intensity at lower temperatures might carry a fitness advantage because cold ants cannot move fast enough to retrieve food sufficient to balance the predation risk associated with foraging.

The metaphor of an adaptive landscape is only one of many ways to consider the relation of phenotype and fitness. Sometimes drawing on this metaphor, the evolutionary advantages of flexibility have been explored in many areas of evolutionary biology (Waddington 1953, Bradshaw 1965, Via and Lande 1985) including behavior (Gillespie and Caraco 1987, Wcislo 1989, West Eberhard 1989). Many of these models emphasize the extent of variability, that is, the magnitude of differences among individuals that changing behavior can produce.

Other models emphasize the time course of environmental and phenotypic change. In these, three types of variables are usually involved, representing the generation time of the organism, the temporal pattern of phenotypic and environmental change, and the relative fitnesses of the possible phenotypes. Levins (1968) used the idea of a "fitness set" to explore the relation between fitness and the dynamics of phenotypic change. Consider two phenotypes (P1 and P2) that occur in two environments: P1 in E1, P2 in E2. The two phenotypes may have similar fitness consequences. If so, and there is a cost to changing phenotype, then as the environment changes from E1 and E2, the organism should adopt an inflexible phenotype intermediate between P1 and P2. In this example the time course of environmental change is unimportant, and phenotypic change is not adaptive. However, suppose the fitness consequences of the two phenotypes are very different. Then the optimal strategy will depend on the time course of environmental change. If the environment alternates rapidly from one to the other of its two states, the organism should specialize on the phenotype with the highest fitness. If the environment changes very slowly in relation to the life history of the organism, then the organism should specialize on the phenotype appropriate for the environment it is usually in. Finally, there will be an intermediate time scale of environmental change at which the organism should be flexible, changing from one phenotype to another as the environment does. Slobodkin and Rapoport (1974) discuss the evolution of flexibility from a similar perspective. One difference, though, is that they consider fitness to be correlated with the time scale of pheno-

typic response; in their view, short-term phenotypic change is inherently less costly than longer-term change.

In N. Moran's model (*unpublished manuscript*) the time scale of phenotypic response to environmental heterogeneity is encompassed by a measure of the accuracy of the match between phenotype and environment. This measure of accuracy incorporates two factors related to time. The first is the predictability or reliability (from the organism's standpoint) of environmental change, which depends on the temporal patterns in which it occurs and in which the organism perceives it. Second, there is the time lag between the environmental change and the phenotypic response. More generally, this lag is the result of what Levins (1968) called the length and complexity of the pathway, which can be genetically, developmentally, and behaviorally mediated, between the environment and the organism's response to it. In Moran's models, frequent environmental change, accurate phenotype-environment matching, and large fitness differences among possible phenotypes can all increase the likelihood that alternative phenotypes will be maintained over evolutionary time. Moran is primarily concerned with the evolution of irreversible developmental switches leading to alternative morphological characteristics. In the case of flexibility, that is, when phenotypic plasticity is reversible, phenotype-environment matching would be even more important.

Theoretically, then, it is clear that the time scale of phenotypic response to changing environments can be important in the evolution of phenotypic plasticity. Theoretical work on this is gradually being extended to include behavioral flexibility as one type of phenotypic plasticity (Brown 1989, West Eberhard 1989). Further empirical work would contribute to this theoretical approach. For behavioral ecologists to elucidate the evolution of behavioral change, we need to know more about how it works: how and when behavior changes, the accuracy of behavior-environment matching, and the time lag between environmental change and behavioral response.

For the ecologist, other questions arise: What are the ecological consequences of behavioral change? How does environmental change affect interactions among species? This means understanding when the relation of the flexible behavioral responses of coexisting species is ecologically important. Many of the variables in ecological models of the population dynamics of interacting species are affected by changes of behavior. One such variable is the functional response of predator to prey (see Chesson and Rosenzweig 1991). Another is the competition coefficient ( $\alpha$ ), which describes the extent to which resource use overlaps (Schoener 1983). If each species' resource use changes when environments do, then the outcome of competition will not be constant.

The study of changing environments spans a broad range of ecological interests. In the relation of phenotypic and environmental change, time scale can be crucial. While behavioral ecology has been more concerned with instantaneous variation than with the transformation of behavior over time, some models in evolutionary ecology emphasize temporal effects. To test these models, we need further empirical study of the dynamics of behavior. The results should contribute to our understanding of how species interact in changing environments.

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