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Behavior and community structure

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Summary. For various reasons, ethologists have paid relatively little attention to the ecological implications of their data and theories. Similarly, ecologists have incorporated few of the results of investigations of animal behavior into their theories and interpretations. I explore two components of animal behavior (habitat selection and foraging behavior) that offer substantial opportunities to enrich and inform theories of population and community ecology. Components of habitat selection theory with major implications for ecological theory include: (a) the willingness of individuals to accept suboptimal habitats, (b) the behavior of individuals when they encounter borders between habitats, (c) how competition among individuals of dominant and subordinate species influences their distribution among habitats, and (d) how animals balance risks of predation and rates of energy intake while foraging. Components of foraging theory that have high potential to inform ecological investigations include: (a) formation of search images in habitats with complex structure, (b) the role of individual history and current physiological status on prey selection behavior, (c) food storing behavior, and (d) foraging behavior and the evolution of mimicry systems. For each of these components I offer suggestions for research whose results would build bridges between ethology and ecology.

Key words: habitat selection, foraging behaviour, community structure, behavioral ecology, review.

Resumen. Por varias razones, los etólogos no han valorado suficientemente las implicaciones ecológicas de sus datos y teorías. De igual manera, los ecólogos han hecho poco uso de los resultados de investigaciones etológicas. En la presente revisión se abordan dos temas de comportamiento animal (la selección de hábitat y el comportamiento de aprovisionamiento) que ofrecen oportunidades substanciales para enriquecer el aspecto ecológico de las teorías sobre la estructura de poblaciones y comunidades. Los componentes del estudio de la selección de hábitat que tienen mayor implicación en la teoría ecológica incluyen: (a) estudios comparativos de la disposición de los individuos a aceptar hábitats subóptimos, (b) el comportamiento de los individuos cuando encuentran los límites de un hábitat, (c) cómo influye la competencia entre individuos dominantes y subordinados en su distribución entre hábitats, y (d) cómo los individuos equilibran el riesgo de depredación y la tasa de ingestión de energía durante el aprovisionamiento. Los componentes de la teoría de aprovisionamiento que tienen mayor implicación en la teoría ecológica incluyen: (a) formación de imágenes de búsqueda en ambientes con estructura compleja, (b) la influencia de la historia de cada individuo y su estado fisiológico actual en la selección de presas, (c) estudios comparativos sobre el almacenamiento de alimentos, y (d) el comportamiento de aprovisionamiento y la evolución de los sistemas de mimetismo. Para cada uno de los temas se sugieren propuestas de investigación que favorecen el acercamiento entre la ecología y la etología.

The context for this review was concisely stated by G. Evelyn Hutchinson with his metaphor “The ecological theater and the evolutionary play.” The actors in the evolutionary play perform a variety of behaviors, and many of the properties of ecological systems are the result of their behavior. Indeed, a major goal of ecology is to determine both consequences of behavior for the structure and functioning of ecological systems and, in turn, the influence of those complex systems on the evolution of the behavioral traits of organisms. Here, I discuss several ways in which behavior influences the structure and functioning of ecological communities, and I suggest challenges for future research.

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Although what I have just stated is generally accepted by scientists today, during much of the past century many students of animal behavior paid little attention to the ecological theater, even though an ecological perspective was central to Niko Tinbergen's approach to animal behavior (Tinbergen, 1951). The view that dominated thinking in the social sciences for many decades was that, although humans had clearly evolved from primate ancestors, human behavior was no longer influenced by human genetics. Behavioral scientists, especially psychologists, engaged in an extensive search for general laws of learning. That search failed in large part because learning is not a unitary phenomenon. It was not until the 1960s that experiments were performed to elucidate how specific features of learning had been molded by the varied problems organisms are trying to solve (García &Koelling, 1966). Today no serious student of animal behavior questions that complex patterns of learning have been molded by environmental problem-solving (Seligman, 1970), so it is difficult to imagine how differently experiments were designed and results were interpreted 35 years ago.

Ecologists, in turn, have had an uncertain relationship with the field of animal behavior. Behavioral ecology has generally been an important component of ecology, but population ecologists have not incorporated the rich results of behavioral ecological research in their models. Papers dealing with behavioral ecology have occupied a decreasing proportion of the programs of the annual meetings of the Ecological Society of America during recent decades. To foster their own interests behavioral ecologists formed their own societies and attended their own meetings.

Part of the reason for the general neglect of behavioral ecology in ecological studies is due to the difficulty of incorporating behavioral data into models of ecosystem functioning. Modelers of complex systems must sacrifice details to make their theoretical and simulational analyses of the major features of the systems tractable. A key factor is that behavioral responses typically occur much more rapidly than rates of change of population parameters. Behavior of individuals has often been sacrificed, partly because of a lack of the necessary species-specific information. In addition, behavioral ecologists have, until recently, given little thought to the broader ecological consequences of the decision rules they have developed to predict and describe the behavior of individuals. Recently, models have been developed that simplify the incorporation of individual-based models into population-level models. They work by analyzing separately processes that operate at different time scales (Fahse et al., 1998).

A major challenge confronting investigators in the fields of behavior and ecology is to find more powerful ways of integrating studies of the ecological theater and the actors that constitute the evolutionary play. In this paper I focus my attention on two components of behavioral ecology whose ecological implications have been most thoroughly explored - habitat selection and foraging behavior. These components illustrate useful approaches for integrating behavior and ecology, and they provide a rich arena for additional predictions and tests.

Habitat selection

The distribution of organisms is determined by two processes. One is the choices made by individuals about where and when to do things. The other is the action of agents that remove individuals from specific places. Among these removal agents are conspecific individuals, individuals of competing species, predators, parasites, and physical events (storms, severe cold, landslides, etc.). I begin by considering choices of individuals, both in the absence of density-related interactions and under competitive intraspecific interactions. Then I consider interspecific interactions, both competitive and trophic. The first theoretical explorations of habitat selection (Fretwell & Lucas, 1970) dealt with density-dependent selection of habitats by individuals of a single species. The individuals were assumed to have perfect information on which to base their decisions (the Ideal Free Distribution). Fretwell and Lucas also developed a model of "despotic distributions" in which less dominant individuals are forced to settle in lesser quality habitats. Subsequent theoretical elaborations of habitat selection dealt with the costs of acquiring information, and the amount of time an individual should use different patches (Charnov &Orians, 1973). Methods have been developed to assess density-dependent habitat selection in species that are difficult to observe directly (Rosenzweig &Abramsky, 1984). The general predictions from these models are that better habitats should be settled first and that higher settling densities in better habitat depress environmental conditions such that expected reproductive success is approximately equal in all occupied habitats.

Time was not a constraint in early theoretical models but habitat selection is typically time-constrained because (a) there is a finite probability of death while searching, (b) habitats may fill up so that better habitats are pre-empted, and (c) breeding success is often reduced by delays. Therefore, natural selection may favor acceptance of a patch that is poorer than the average suitability of all available patches at the time the choice is made. This may be one reason why so many organisms have evolved to use familiarity with a site (having bred there before or having been raised there) as a basis for selecting a breeding habitats rather than taking time to engage in a more thorough search. Specific predictions from these models that need additional testing include: (a) The shorter the breeding season, the more readily individuals should accept poorer quality habitats. (b) Intraspecific competition should expand the range of habitats used by individuals of a species. Conversely, when population densities are reduced, the range of a species and the array of habitats it uses should contract.

Dispersal in habitat mosaics

Dispersing individuals seek appropriate habitats while moving through a mosaic of different habitat types. The probability that they will find a suitable habitat depends on both the distribution and prevalence of suitable habitats and on the behavior of individuals at habitat boundaries (Haddad, 1999). An individual may either maintain its direction of movement when it encounters a boundary or turn abruptly to remain within its current habitat patch. The probability of each type of response is likely to depend on the relative quality of the newly encountered habitat and the risk of moving though it. The poorer or riskier it is to move in it, the more reluctant the individual should be to enter the habitat. Therefore, the behavior of individuals at habitat boundaries should exert strong influences over the probability that habitat types are entered and the likelihood that individuals will traverse corridors of suitable habitat to find other patches of suitable habitat (McIntyre &Wiens, 1999). Because empirical studies of the behavior of individuals at habitat boundaries are few, the value of additional studies on a variety of species is high.

Interspecific interactions and habitat distributions

Intraspecific competition may force subordinate individuals to accept poorer quality habitats, but the highest settling densities are nonetheless expected in the best habitats. In contrast, interspecific competition may result in either the exclusion of a species from its preferred habitat or in each species becoming a specialist on its preferred habitat type (Lawlor & Maynard Smith, 1976).

Interspecific interactions are known to influence patterns of spatial occupancy in a wide range of animals, including mammals (Brown, 1971; Brown & Munger, 1985), birds (Catchpole, 1973; Cody, 1978, 1979; Feinsinger, 1978; Hogstad, 1975; Leisler, 1988; Reed, 1982; Robinson & Terborgh, 1995; Saether, 1983; Sorjonen, 1986; Tiainen et al., 1983; Willis & Oniki, 1978; Wolf et al., 1976), lizards (Pacala & Roughgarden, 1982), and insects (Lawton & Hassell, 1981).

A useful graphical method for visualizing and analyzing habitat selection under conditions of competition uses a technique known as "isoleg" analysis, after the Greek words for equal (*isos*) and choice (*lego*). An isoleg is a line in a state space of animal densities such that some aspect of a species' habitat selection is constant at every point on the line (Rosenzweig, 1981). The first isoleg analyses supported the results of Lawlor & Maynard Smith (Rosenzweig, 1981). Subsequent analyses, which incorporated interference competition into the models, yielded the surprising result that individuals of a subordinate species may actually preferentially select a less optimal habitat when of a competitor is present (Pimm & Rosenzweig, 1981). A field test of habitat selection among hummingbirds confirmed these theoretical predictions (Pimm et al., 1985; Rosenzweig, 1986), but many more field tests are needed to determine whether this is a peculiar property of exploiters of nectar or is widespread among a variety of species.

Interspecific territoriality, a particular form of dominace behavior in which individuals of a competing species are systematically excluded from particular areas, has been demonstrated in a number of studies of temperate zone birds (Catchpole, 1978; Catchpole & Leisler, 1988; Cody, 1974; Murray, 1971; Orians & Willson, 1964; Rice, 1978). Recently, Robinson & Terborgh (1995) have shown that interspecific territoriality is widespread among congeneric species of birds in the Peruvian Amazon.

Because individuals of a larger dominant species need to harvest energy at a higher rate than individuals of a smaller species, many environments might be unable to support individuals of the dominant species (Morse, 1971, 1974, 1976). If so, dominant species would be restricted to habitats of high productivity, and removal of individuals of the dominant species would allow individuals of the subordinate species to occupy the vacated habitats but removal of the subordinate species would have little effect on the distribution of the dominant species. The results of Robinson & Terborgh (1995) support these predictions and agree with previous studies demonstrating that interspecific aggression is typically asymmetrical, with the larger species dominating the smaller (Leisler, 1988; Prescott, 1987). However, many more removal experiments are needed in habitats of varying quality.

Dispersal and coexistence

Many models suggest that a species that would be eliminated competitively from an area may persist if its offspring dispersed more widely than the competitive dominant. Most of these models are not spatially explicit; that is, only distance from the natal site is included in the models. However, incorporation of spatial dimensions into the models does not alter the general theoretical result (Holmes & Wilson, 1998). Most empirical examples come from plants whose dispersing propagules cannot actively choose the distance they will move or where they will settle. As yet to be investigated for animals is whether individuals of poor competitors actually avoid settling in good patches close to their natal sites. Do they bypass them to settle in more distant sites of equal quality? And if they do, what are the circumstances that favor such selectivity?

The basic condition that must be fulfilled for such behavior to be advantageous is that the probability that a site will be colonized by individuals of the dominant species declines with distance from the natal site of the dispersing individuals of the subordinate species. This condition is unlikely to be met universally, but no analyses of the conditions under which it is likely to be met have been carried out. Results are likely to be sensitive to the composition and spatial distribution of habitat patches.

Predators and habitat selection

If the best places to forage are also the safest, predators should have little influence on distributions of foraging individuals of their prey. However, because of their intrinsic structure or distance from safe retreats, good foraging areas are often riskier places in which to forage than are poorer foraging sites. For example, small desert rodents that are highly vulnerable to attacks by owls at night tend to forage mostly under the canopies of shrubs, whereas the larger kangaroo rats, that have better developed escape behavior forage more frequently in open areas between shrubs (Brown & Zeng, 1989). Trapdoor spiders that live in areas with high densities of prey typically wait for prey individuals to come close enough to be captured while the spider maintains contact with its burrow entrance with its hind legs. Species that live in more arid environments with lower densities of prey pursue prey at greater distances from their burrows (Main, 1957).

The role of predators in influencing habitat use is amenable to experimental manipulation. In addition to experimental approaches, comparative studies of habitat use by a species in areas with high vs. low densities of predators can be used to assess how individuals trade-off reducing predation risk and achieving high rates of energy intake.

Foraging behavior

Optimality modeling has been the method most extensively used in the development of foraging theories. Optimality modeling has proven to be especially useful because it provides a quantitative way to combine decision assumptions, currency assumptions, and constraint assumptions into single models that yield testable predictions about how foraging animals should make decisions (Stephens & Krebs, 1986). Most of the important advances in our understanding of animal foraging have resulted from experiments that have tested explicit predictions from optimal foraging models.

Interestingly, the first papers on foraging theory had as their goal the elucidation of patterns of community structure (Emlen, 1966; MarArthur & Pianka, 1966). During the subsequent two decades, optimal foraging theory focused primarily on the study of autecology (Stephens & Krebs, 1986); only recently has it been used to address problems of ecological relationships such as competition, predation, and trophic dynamics (Werner, 1977; Belovsky, 1984).

Real predators make many decisions about where to forage, which prey to pursue and capture, how much of a prey item to eat, when to leave a patch to seek alternative foraging sites, and whether to bypass a suboptimal patch to continue searching for a better one. Foragers may form search images that increase encounter rates with some prey types at the price of reducing encounter rates with others. In structurally complex environments individuals may use different search modes, searching selectively for prey on specific structural elements of the environment.

In marked contrast, competitors, predators, and their prey, as characterized in standard competition and predator-prey equations, generally lack any interesting behavior. In these equations, predators do not actually select among prey types or change diets in relation to prey abundances. In addition, prey lack interesting antipredator behavior (Lima, 1998b). Also, most models of metapopulation dynamics assume constant probabilities of dispersal and recruitment. These deficiencies in standard population models are serious because models that incorporate such complex behaviors, which are predicted by all foraging models (Charnov & Orians, 1973; Stephens & Krebs, 1986), lead to different predictions about population dynamics (Fryxell & Lundberg, 1998). Moreover, adaptive anti-predator behavior can stabilize oscillating predator-prey dynamics (Ives & Dobson, 1987; Ruxton, 1995; Crowley & Hopper, 1994). Contrary to the general theoretical result, two predators may coexist on a single prey type if they employ different foraging modes (Wilson et al., 1999).

Fortunately, ecologists are now investigating the ecological consequences of the behavioral complexity of behaviorally complex foragers in varied environments. For example, the influence of individual behavior on population dynamics and population stability has been explored theoretically by Fryxell & Lundberg (1998). I will cite other examples in subsequent discussions.

Herbivores have long been known to influence the composition of plant communities, but details of the effects of selective grazing and browsing are as yet poorly known. Interestingly, an optimally foraging herbivore in a seasonal environment is able to promote coexistence among many plant species. The mechanism involves diet switching as plant densities change (Hambäck, 1998). Belovsky (1986a, 1986b) used linear programming models to investigate foraging by herbivores of varied sizes. Constraints on their foraging were determined by minimum digestibility of different plant species, sizes and abundances of food items (which determine cropping rates), capacity of the animal's digestive system, and turnover rate of food in the gut. Belovsky's analysis, combined with field experiments, suggested that the structure of herbivore communities may be strongly influenced by foraging behavior and foraging energetics.

Size-selective predation

The best-known example of the role of choices by predators on the structure of ecological communities is the influence of size-selective predation on the composition of zooplankton communities in lakes. The process, first described by Brooks & Dodson (1965), is driven by the fact that large zooplankters are superior competitors in exploitation competition (MacIsaacs & Gilbert, 1989), but are preferred prey for planktivorous fish. As a result, large species of zooplankton dominate fishless lakes but small species of zooplankton dominate lakes with fish.

Selection of prey may change with a predator's age and experience. Individuals differ from one another both genetically and, as a result of their prior experiences. Therefore, information about morphology and the prior histories of individuals should be gathered and incorporated into predictions about their varying responses to foraging experiments. For example, D. S. Wilson (1998) has shown that the great morphological and behavioral variability that exists within single populations of bluegill sunfish influences where they forage and the food they eat.

Typically, however, experimenters have assumed that all individuals used in an experiment are the same and that they perceive the objectives of the experiments the same way – the way the experimenter does. This assumption is certainly false. How animals perceive experimental situations, how their perceptions vary over time, and the possible genetic underpinnings of this variability remain major challenges for future research on foraging behavior.

Disease and prey selection

An interesting possibility, as yet little explored, is that predators do better if they eat individuals of the same or closely related species than if they eat individuals of more distantly related species. Individuals of closely related species, because they are biochemically very similar to the predator, may be more likely to have good balances of nutrients. However, this potential advantage may be offset by the fast that close relatives are more likely to harbor parasites that can infest the predator. There is experimental evidence that predators grow faster when fed closely related prey than when fed more distantly related prey (Pfennig, 2000; Toft & Wise, 1999). However, the life cycles of many parasites include hosts that are very distantly related, so the generality of the result is questionable. Predators are expected to evolve abilities to discriminate among healthy and sick prey, especially among closely related species. How much and in what ways pathogens influence predators' choices of prey is easily investigated experimentally. If genetic relatedness and health status of prey strongly influence predator behavior, these factors may exert an influence on habitat distributions of predators and their prey.

Food storage

Among the ways that animals deal with fluctuations in food availability is to store food. Food may be stored within an individual's body, typically as fat among animals but also as carbohydrates among plants. Storing food outside the bodies of organisms is favored in cold and arid environments because decay by bacteria and fungi is slow in under those conditions. Also, some food types, notably seeds, spores, wood, fungi, leaves, and nectar, are more readily stored than others, either because they already have a low moisture content or because they can be dried prior to storage.

External storage of food clearly allows many species to persist in environments where they could otherwise survive only seasonally or in resting states. However, little is known about the role of food storage in influencing the structure of ecological communities. Does food storage result in increased species richness in many communities? If so, which ones? Is the number of food-storing species that can live together influenced by the variety of sites in which food can be stored? Do individuals store food in places less likely to be visited by individuals of other species?

Foraging and habitat structure

Habitat structure influences movement options (which differ in terrestrial and aquatic environments), visibility (distance prey can be detected), and the ability of predators to make discriminations among prey types. In structurally complex environments prey may be found in many places that differ with respect to the ease with which a predator can search in them and how well the prey match their backgrounds. Therefore, habitat structure can potentially determine the number of "efficient" foraging modes, home range sizes, and the number of species an environment can support.

Foraging theory suggests that the concept of prey density is of little utility. Predators do not know what prey densities are; they know only their encounter rates. A predator searching in a structurally complex environment is likely to selectively locate and consume prey that are more conspicuous to it, either because they are located in places more easily searched by the predator or because they match their backgrounds more poorly. Over time the result is a reduction in the fraction of prey that are situated in more conspicuous places. The predator experiences this as lower encounter rates with prey (prey depression). If the prey selectively recruit into sites where their probability of being captured is lower, rates of prey capture are likely to remain low for some time.

In response to prey depression in complex environments, predators have two options. First, they could adopt alternative search modes that enabled them to find prey in other sites more efficiently than is possible using the first foraging mode. Second, they could expand the area over which they hunt so that they forage less often over the same piece of ground.

If there were only a single species of predator, the expected result would be an evolutionary arms race in which the prey evolved to be increasingly more difficult for the predator to locate while the predator evolved to become increasingly more effective in locating prey with their new characteristics. However, if another species of predator were present that was more effective in finding prey in a different part of the environment than the first predator, then the arms race should stabilize. The prey should more poorly match either feature of its environment than would be the case if there were but a single species of predator. Similarly, if there are multiple species of prey, each of which requires a different morphology and searching behavior on the part of a predator for efficient capture, the optimal phenotype for a predator is one that is less effective on any prey type than a specialist on one of them.

This line of thought suggests some interesting questions for future research. What is the relationship between habitat structural complexity and the number of different efficient foraging modes within it? Do predators of different species mutually reinforce one another's foraging success by evolutionarily "driving prey into one another's jaws?" The first question can be investigated both in the laboratory and in the field. Investigating the second question, which postulates evolved responses, will require field studies in environments with different compositions of predator species

Learning, prey choice, and community structure

Some specialized predators have genetically determined foraging behavior and methods of prey identification. However, most generalized predators must learn the characteristics of desirable and undesirable prey. As a result, the predators seeking prey are likely to be a mixture of individuals that are experienced and naïve with respect to the traits of their potential prey. Predator naivete allows the persistence of prey types, such as flowers that mimic female insects, and flowers and fruits that provide no rewards. Thus, there is reason to believe that the number of species in at least some ecological communities is greater than it would be if there were no naive predators. Learning has been extensively investigated for pollinating insects, but how learning influences species composition and abundances of animal-pollinated plants as still unknown.

Behavioral responses of prey to predators

The previous section, as is typical of most analyses of predation, focused on the lethal aspects of predation, that is, the consumption of prey individuals. But in addition to killing them, predators stimulate behavioral changes in their prey. These changes may have large influences on ecological communities that differ from those caused by consumption (Lima, 1998a, 1998b). In addition, because most animals are both predators and prey, the behavior of predators is molded by the risks they assume by seeking and pursuing prey.

Prey may respond directly to the presence of a predator, but they may also estimate the general level of risk of predation and alter their foraging behavior accordingly. The accuracy of their estimates and the time lag between a change in the risk situation and the prey's new estimate have substantial influences on the dynamics of predator-prey interactions (Luttberg & Schmitz, 2000).

The most frequently employed method of determining how animals balance safety against finding food is to deprive them of food. Virtually all experiments have demonstrated that hungry animals assume more risks to acquire food than sated animals do (Lima, 1998a). Because most of these experiments were conducted in the laboratory, they could not demonstrate that reduced risk-taking actually led to reduced mortality, but a few field studies have shown reduced mortality (Lima, 1998a) or slower growth rates (Skelly & Werner, 1990; Persson & Eklov, 1995) among risk-aversive predators.

Such behavioral decisions clearly have population-level consequences, but demonstrating those consequences is difficult. The most readily detected effect is to change the distribution of prey over landscapes. For example, predator-induced emigration from pools is widespread among stream-inhabiting animals (Wooster & Sih, 1995). Relatively immobile predators may induce prey emigration more consistently than do predators that more readily follow their prey.

Although it is clear that anti-predator responses of prey can and do influence distributions of prey, little is known about the effects of these interactions on entire populations. For example, predators might only redistribute animals among habitat types without altering population sizes. Or they might initiate a series of events that culminate in significant changes in overall population sizes and densities. A major challenge for future research is to determine the relative frequency of such effects in nature and, more importantly, why they occur. Similarly, we need clever research and theoretical analyses to help assess the relative importance of lethal and nonlethal effects of predation on ecological communities.

Evolutionary responses of prey to predators

That prey evolve in response to the activities of predators has long been known by biologists. Mimicry was the first example of an evolutionary outcome of interactions among predators and multiple prey to be investigated. Organisms can and do mimic a variety of objects. Which objects can be mimicked depend on the sizes and shapes of both the objects and the potential mimicking organisms. Some objects, such as spheres and flat surfaces are difficult to mimic. Also organisms can mimic a portion of an object, an entire object, or a collection of objects. Details of the mimicry and the environment in which it is functioning influence the distance at which mimics can be detected and the efficacy of different escape responses when the individual has been detected by a predator.

From the perspective of prey, complex environments afford a rich array of structures to mimic and places in which to hide from predators. If many prey species use the same mechanisms to escape from predators, predators should be able to learn to exploit all species more efficiently. Selection by predators is thus expected to lead to a diversification among prey species with respect to escape mechanisms and a relatively uniform distribution of prey within what is known as the available “escape space” (Ricklefs & O’Rourke, 1975). This interesting possibility has received little attention except for a few papers about what has been termed the “aspect diversity” of cryptic insects (Rand, 1967). Whether the concept applies to vertebrate prey or in aquatic environments is still unexplored. The possibilities for creative experimentation and assessments of patterns are enormous. Also, given that predators learn the escape responses of prey and adjust their attack strategies accordingly, one might expect widespread escape behavior polymorphisms among insects, but this appears not to be the case. Why this is so is not clear.

Relative abundances of models and mimics are important in the evolution of Batesian mimicry systems (Wickler, 1968). For Müllerian mimicry, however, it has been generally assumed that the relative abundances of the species were irrelevant because all members of the complex are assumed to benefit from learning by the predator. However, this argument neglects selection for detoxification by predators and provides no explanation why Müllerian mimicry systems in a given locality have only a few species in them.

The following hypothesis proposes an approach to this problem. At the beginning of the evolution of a Müllerian mimicry system, some of the prey are presumably only slightly toxic, but the energy losses to a predator from eating the slightly toxic prey would be small. However, as the number of species in a mimicry system increases, the losses in foraging efficiency for predators also increase, for several reasons. First, the total prey recognition time of a predator increases because a higher fraction of the total prey it encounters will be members of the mimicry complex. Second, Müllerian mimicry complexes often have Batesian mimics associated with them. As the size of the mimicry complex grows, it will pay for the predator to be able to make finer discriminations among members of the complex. Third, the protection of the mimicry complex may result in larger populations of the constituent species, possibly at the expense of palatable prey in the same area. This increases the potential benefit to a predator from an ability to detoxify one or more members of the complex. The most likely member to be detoxified first will be a large, common one.

Thus, a point may be reached at which tolerance of a toxin or detoxification of the defenses of a member of the mimicry complex are favored. Nevertheless, predators should have difficulty in discriminating the new palatable members from the others and are likely to sample many individuals in the process of learning. All well-adapted members of the complex are likely to be vulnerable at this point since they will have evolved a set of behavior patterns based on their seldom being attacked. Therefore, if pursuit times are short and the probability of capture is high given a decision to pursue, predators may find it profitable to pursue and capture many individuals and to discard the unpalatable ones rather to spend a great deal of time attempting to make finer discriminations among members of the complex.

If these arguments are approximately correct, it follows that the limits to Müllerian mimicry complexes may be set by a threshold of detoxification by a significant predator, which initiates a rapid disruption of the complex. Thus, Müllerian mimicry complexes may undergo a long term cycle that begins with a slow process during which mimicry is improved and more species are added to the complex, followed by a rapid break-up, followed by a another slow reconstruction of the complex. Testing this hypothesis would be difficult, but the prediction that species in large mimicry complexes are more often attacked than species in small mimicry complexes could be tested in the field. Also analysis of museum specimens gathered during the nineteenth century might reveal changes in the composition of those complexes.

Interestingly most cases of mimicry and most studies of aspect diversity of prey involve responses of insects to vertebrate predators, all of which capture prey at high rates and, consequently make many rapid prey choice decisions. A promising area for behavioral research is to investigate the applicability of general mimicry ideas to prey that are large relative to their predators. This includes evolved responses of arthropods to their arthropod predators and vertebrates to their vertebrate predators.

Behavior and speciation

Both behavior and development are condition-sensitive; that is, different complex phenotypes are produced by a single genotype. The possibility that major evolutionary divergence may regularly originate as a bifurcation in behavioral patterns has been explored by West-Eberhard (1986, 1989, 1992). She proposed that behavioral novelties can explain the origin of facultative worker behavior in wasps and bees, and she argued that the new behavioral phenotypes can evolve semi-independently within a single species.

There are several reasons why plastic behavioral traits are likely to be important initiators of new directions in evolution. First, behavior is more labile than morphology. For every morphology there may be several optimal behaviors. The reverse is seldom true. Second, because of the greater abundance of potential cues for regulating the expression of an immediate behavioral adaptive response, adaptive behavioral plasticity is expected to evolve more readily than does adaptive morphological plasticity. Third, behavior during development can greatly influence morphology.

Therefore, behavior may accelerate the rate of speciations, especially among organisms with complex behaviors. This suggestion is supported by phylogenetic analyses suggesting that speciation rates are higher in lineages with strong sexual selection (Lande, 1982; Barraclough et al., 1995).

If behavior does stimulate speciation, it may, for several reasons, have indirect effects on the composition of ecological communities. First, regional species richness influences local species richness, even though the processes by which it does do are not well understood (Ricklefs, 1987, 1989). Therefore, by promoting speciation and an increase in regional species pools, behavior could result in an increase in the number of species living together in local ecological communities. Second, behavioral flexibility may result in the occupation of habitats not previously used by a species. Acceptance of a new habitat or development of a new way of foraging may, in turn, result in the expansion of the range of a species. Such range expansions may happen suddenly, as illustrated by the invasion of Western Europe by the Collared Dove during the past 50 years.

Concluding remarks

My cursory review of the implications of habitat selection and foraging behavior for the structure and functioning of ecological communities demonstrates the existence of vast, untapped potential for behavioral research. Research is needed to determine more precisely under which conditions different types of behavior have the greatest influence on population dynamics and on the structure and functioning of ecological communities. Also, I have considered only two types of behavior, although they are likely to be the most important ones with respect to influencing ecological communities. However, the ecological roles of social organization and mate selection, for example, have been little explored. The behavior of the players in the ecological theater needs to be much better understood if we are to fulfill the promise of Hutchinson's apt metaphor.

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