

Forum: Invited Review

# The fusion of behavioral ecology and ecology

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Behavioral ecology and ecology have projects in common. Community ecology can provide behavioral ecology with the tools to ask realistic questions about the current action of natural selection. Evolutionary ecology has moved beyond asking “Why does trait  $x$  contribute to reproductive success?” and on to “What are the conditions under which trait  $x$  contributes to reproductive success?” We need to bring this ecological perspective to the study of the evolution of behavior. Community ecologists have recognized that behavior influences ecological outcomes. For example, behavior contributes to the effect of history on community assembly, to indirect effects in predator–prey interactions, and to the responses of populations to human disturbance. More generally, behavior is often the source of context dependence; behavioral responses in different conditions lead to different ecological outcomes. As community ecology is broadening to include behavior, behavioral ecologists can begin to incorporate ecological perspectives in asking evolutionary questions. [*Behav Ecol* 22:225–230 (2011)]

Behavioral ecology and ecology need each other. Behavior is linked to ecology at every level, from the population to the ecosystem, but here I will focus on the relation of behavior to population and community ecology. Behavioral ecology joins the study of animal behavior to evolutionary biology; its goal is to explain how behavior determines fitness. The goal of ecology is to explain the outcomes of interactions of organisms with their environments, including other organisms. Ecology, especially community ecology, can provide behavioral ecology with the tools to ask realistic questions about the evolution of behavior. In turn, the study of behavior can help ecology deal with questions about context dependence.

## ECOLOGY AND THE EVOLUTION OF BEHAVIOR

In the first half of the 20th century, studies of behavior and of ecology were more intertwined than they are now. It was taken for granted that an animal’s behavior could be understood only in the context of its natural history. To pursue evolutionary questions about behavior, we now need to bring back analytical natural history.

Consider a 1938 study, published in the *Journal of Mammalogy*, which examines the feeding behavior, the construction of large mounds of twigs as nests, and the mating behavior of the dusky-footed wood rat in northern California (Vestal 1938). The article is called “Biotic relations of the wood rat (*Neotoma fuscipes*) in the Berkeley hills,” and it lives up to its title, outlining the animal’s biotic relations by counting how many nests are near which plant species, how many sightings of the rats eating involve which food source, the distances among nests, and how these measures depend on season and habitat. In their 1951 book, Linsdale and Tevis (1951) did all this for a larger population and a longer time, tracking the housing, movements, feeding, and reproductive behavior of a population of wood rats in a reserve in California.

The early ethologists emphasized the importance of field observations like these, and even when ethology morphed into the field of animal behavior, with an increasing emphasis on physiology, no one questioned the value of learning about animals in their environments. But as we began to aim for generality, using experimental designs that permit statistical analysis, and as it became technically possible to learn more about the physiology of behavior, natural history lost its panache. Natural history was anecdotal; experiments were real science.

Thus, in a 1982 study of dusky-footed wood rats, published in *Animal Behaviour* (Wallen 1982), careful field measurements of which individuals were observed in which nests are followed by a series of laboratory experiments measuring the extent of aggressive behavior between female–female, male–male, and male–female pairs. For me, the most intriguing result was that there are common nests, like pubs, where wood rats go to visit each other and then go back to their own nests. The laboratory experiments showed that both sexes distinguish between familiar and unfamiliar individuals of the same sex. Some females were more active than others; in the field, more active females might do more visiting.

Now suppose in 2010, a researcher sets out to learn more about dusky-footed wood rats. One question is whether a certain behavior promotes reproductive success, for example, whether more active females do more visiting and have higher reproductive success. This evolutionary question would be best answered by going back to extend the work begun in the 1938 study to answer ecological questions such as the following: How do the visiting relations, female activity levels, or aggression between males depend on habitat, season, and food availability? In what conditions do alliances among females promote the survival of their offspring?

The answers to evolutionary questions about animal behavior always depend on the animal’s ecology. Behavioral ecology began in the mid-70s with simple optimization models drawn from economics. It seemed at first as though these simple models would have great explanatory power. But when we investigated the fit between a simple model and behavior, things turned out to be more complicated. Of course, this is always true; even the correct simple model of anything biological cannot possibly match the real system. Richard Levins described this neatly (Levins 1968): every model, even if it describes correctly the relevant relations among factors, is either so detailed that it does not tell you anything you do not already know or so general that it cannot explain any specific case, and all modeling is the tension between these 2 extremes. In behavioral ecology, though, it is clear that what is needed in the middle is ecology.

For example, the early models of the foraging–vigilance trade-off began with a simple premise. Either a bird can face down and eat, pecking on the ground, or it can look up to see if a predator is approaching. A bird can spend more time eating if another bird will issue a warning when it sees a predator, because then the watcher can take a turn eating itself. In this way, a bird in a group might be able to spend more time

eating than a bird alone. The models that describe this trade-off were elegant. Real birds, however, did not behave exactly as predicted, because birds do other things besides eat and watch out for predators. Other factors, such as temperature, wind, rain, vegetation, parasite load, other animals, human disturbance—to list only a few—affect interactions among birds. The abundances of food and of predators change in time and space. The predictions of the simple models did not fit because rest of the birds' ecology can override the pressures of the foraging–vigilance trade-off.

The essence of the standard evolutionary argument in behavioral ecology is that animals that behave a certain way have higher reproductive success. Behavior is associated with some measure taken to correspond to reproductive success: number of mates, food obtained, or a more direct measure such as number of offspring. We look for the correspondence between variation in behavior and variation in outcome. The bird that fights harder gets to mate more often than less belligerent birds. The wild dog that hunts with others gets more food than the one that hunts alone.

The main reason that the simple economic models of early behavioral ecology did not work is that everything keeps changing. How an individual's characteristics determine its reproductive success is a consequence of its ecology and its web of interactions with others and with the world. When one part of the web changes, it alters the rest. The evolution of any particular trait does not occur against a fixed background in which it is good to be one way and bad to be another. Instead, it must depend on the action of forces that act in context-dependent ways, and the context constantly shifts.

What favors reproductive success in one situation does not in another. For example, studies of sexual selection in some bird species have led to contradictory results. Female choice appeared in some cases, but not others, to depend on the plumage color of males. It was not clear whether plumage color was related to the health of the male, territory of the male, or in fact to any characteristic of the male that might influence the reproductive success of the pair. The arguments became increasingly tangled: the male's plumage color makes him appear as though he can win a fight, which allows him to fight less, and natural selection drives the female to choose him because if his appearance allows him to fight less he will have more time to find food—but maybe the tougher looking male does not really spend more time finding food, and so on. The point here is not to discuss the content of these arguments but to note that they are convoluted, and to suggest that this is because successive studies keep revealing new ecological relations. The more we learn about the reproductive behavior of a particular species, the more it seems that mate choice is related to other aspects of the birds' lives, and that sexual selection is a response to ecological processes (Cornwallis and Uller 2010).

For example, recent work on the pied flycatcher shows that many characteristics of the male are involved in mate choice (Sirkia and Laaksonen 2009). Population genetics studies show that selection has proceeded differently in different parts of Europe (Lehtonen et al. 2009). Young males can learn their songs, which they use when mating, from another species, the collared flycatcher, when it is nearby (Eriksen et al. 2009), so song depends on the local distribution of the 2 bird species. Factors that affect the value of a male's territory, such as parasite load in the nest (Moreno et al. 2009), differ on small spatial scales. Thus, how females choose males in pied flycatchers is embedded in ecological relations that differ across time and space, which determine the consequences of fighting between males and the effects of parental care (Roughgarden et al. 2006) on nestling survival.

## VARIATION

Behavioral ecology needs the perspective of evolutionary ecology to move beyond speculative accounts of what may have happened in the course of evolutionary history. Accounts that use current observations to reconstruct the past action of natural selection are always problematic. If anything back then was different from the way things are now, as it must have been, then even if a trait could have been the same back then, its ecological context was different. When it comes to behavioral traits, we cannot even tell how the trait was different back then, except by using comparative phylogenetic methods (e.g., Grether et al. 2009; Stang and McRae 2009; Tobias and Seddon 2009). Until someone discovers a fossil record for behavior, we can in practice investigate only what are the ecological consequences of a trait now—that is, the evolutionary ecology of behavior.

The perspective of evolutionary ecology starts with explicit attention to variation among individuals. If we can find a current association between variation in behavior and some outcomes, we can go on to ask whether evolutionary change is acting now, as we watch. But if there is not much variation in behavior, we can only speculate about how things might be otherwise. For example, suppose it could be shown that if certain birds did not forage in flocks, they would have to spend more time looking up for predators. It might be that sometime in the past, birds foraging alone starved or got eaten, so that now all that is left are the ancestors of the flocking sort—but maybe not.

Behavioral ecology has an ambivalent relationship with variation. If we hope for a general rule that explains why a certain behavior promotes reproductive success, we are hoping to explain the behavior of all individuals or an average individual. An explanation for why individuals do *x* does not consider individuals that do not do *x* or do it only sometimes. Thus, many studies seek to show that the individuals of a certain species tend to behave in an adaptive way, and variation is beside the point.

Behavioral ecology's attitude to variation comes to it through its parent, ethology. The early ethologists were not much interested in characterizing the nature and magnitude of variation. Instead, the goal was to describe the stereotypic behavior characteristic of the whole species. For ethology, each individual represents its species. The individual, and by extension the species, has a fixed set of behaviors, and if you watch long enough, you will see all the behavior on the list.

This is not to say that behavioral ecologists have always ignored variation in asking evolutionary questions. There is growing interest in measuring how much, and how persistently, individuals differ in behavior and in the reaction norms of behavior (e.g., Lott 1984; Dingemanse et al. 2004, 2010). It takes long-term studies of populations of individuals to learn how differences among individuals are related to differences in outcome such as reproductive success. There are a few outstanding examples. One is the Altmanns' study of the baboons of Amboseli, which (among other themes) shows how variation among individuals is related to social status and to changes in food supply, which together influence how selection shapes life history, reproductive behavior, and parental care (e.g., Altmann 1998; Altmann and Alberts 2003; Nguyen et al. 2009). There is also a body of theoretical work in behavioral ecology that addresses variation directly. For example, frequency-dependent selection leading to an evolutionarily stable strategy (Houston and McNamara 1988) assumes at least 2 variants and a situation in which the proportion of each makes a difference to the fitness of both.

Evolutionary ecology takes variation as a starting point because its attitude toward variation comes to it from its parent,

community ecology. Community ecology deals with populations, characterized by means and variances. Any data point is only one in a cloud of points, not representative of the cloud. This is more realistic than ignoring variation altogether. But looking at variation, the differences among a group of snapshots taken at the same time, is only the first step in investigating the ecological relations characteristic of a phenotype. The next step is to look at change, and this is where the study of behavior contributes to ecology.

### CHANGE AND CONTEXT DEPENDENCE: WHY ECOLOGY NEEDS BEHAVIORAL ECOLOGY

Behavior is important for ecology because many ecological outcomes are the result of behavioral processes. The interactions of organisms and their environments arise from behavior. Behavior produces the predator-prey interaction: a predator catches, finds, and eats its prey and the prey avoids the predator, at least often enough to persist. To learn about this interaction, the ecologist samples numbers of predators and numbers of prey, so as to find the function that relates the 2 numbers, the functional response. The numbers of predators and numbers of prey are the outcome of behavior, how the predators find their prey and how the prey hide or escape. Behavior produces mutualistic interactions. A colony of ants lives in a hollow domatium in the branch of a tree, eating the honeydew of scale insects that feed off the tree, and defending the tree from herbivores. The ant colony's growth determines its behavior, especially the behavior involved in patrolling the tree and attacking herbivores. The effectiveness of the colony's defense behavior, which promotes tree growth, depends on scale density, which limits tree growth. The ants' behavior is the link that produces the functional relations between the tree, ant, and scale populations (e.g., Pringle et al. 2010). In general, behavior generates ecological relationships, or to put it another way, ecological relationships are expressed as behavior.

The ways that behavioral ecology can contribute to ecology, especially community ecology, center around the cluster of issues related to context dependence: variation, change, dynamics, and history. Over the past 10 years, community ecology has grappled with the realization that broad generalizations are always undermined by context dependence. As Heithus et al. (2009) put it, "Context dependence has hindered the development of a general framework for predicting the nature and extent of (risk effects)." I put brackets around "risk effects" because although this statement happens to be about risk effects, the same could be said of the difficulties of generalizing about almost any ecological outcome. As Lawton (2000) points out, ecological outcomes for a particular species in a particular place rarely produce general principles. Environmental change leads to ecological and evolutionary shifts, so that "the local rules of engagement within a community must also change, often gradually but sometimes very quickly. Hence hard won local insights from studies in community ecology are essentially ephemeral."

Context dependence is an inconvenience if we want to build theory about an appealing world that does not exist, a world in which the rules of engagement do not change. In this garden of Eden, or more recently in the forest of Pandora, if you can specify the entire web of interactions among all the players, you will understand everything well enough to predict what will happen. This was the world that the field of ecology began with, the world that Elton (1958) worried would be lost to invasive species, the world in which there would be a single coefficient that relates the number of species to the area of an island. The counterargument that ecological outcomes are determined by random processes (e.g.,

Simberloff and Moeklen 1981; Hubbell 2001) is in part a reaction to the unrealistic vision of this orderly world. In the real world, context dependence is not a hindrance to understanding; it is the way things are.

It is because the local rules of engagement in ecology can change, that it appears that selection shifts in time and space. This is why the behavioral ecologist who studies the ecology of a trait in one time and place will find that the outcomes differ in another. The main project of evolutionary ecology is to understand when and why this happens (e.g., to choose one study out of many, Schemske and Beirzychudek 2007). The effects of local conditions on species interactions create different ecological pressures in different places, and this produces the spatial mosaic of diversity (Thomson 2005).

Unlike behavioral ecology, evolutionary ecology has moved beyond asking "Why does trait x contribute to reproductive success?" and on to "What are the conditions under which trait x contributes to reproductive success?" Evolutionary ecology began with studies of local adaptation in plants (e.g., Clausen et al. 1947). Perhaps, the recognition that ecological pressures vary with conditions came first in studies of plants because it is easy to do transplant experiments. This is more difficult, though not impossible (e.g., Stamps and Swaisgood 2007), with animals who do not stay where you put them and have inconveniently long generation times, but evolutionary ecologists have found other ways to demonstrate local adaptation in animals (e.g., Price et al. 2003; Grether et al. 2009). Perhaps, we are more eager to find invariant truths about the evolution of animal behavior, which seems to parallel ours, than about the evolution of plant traits: there is less at stake in whether a flower should be blue or white as in whether cooperation promotes fitness, or whether females should have many sexual partners.

If there are any local rules of engagement in ecological communities, they are rules about how engagement changes in response to conditions. Curiously, this insight, at which ecology arrived through decades of measuring variation and population dynamics, is natural to anyone who observes behavior, even though the study of dynamics is not explicit in many studies of behavior. Watching animals in the field, what you see is behavior that changes in response to changing conditions.

The ecological rules of engagement often change because of behavior. Context dependence in ecology is produced by behavior. Ecological interactions are influenced by behavior, and behavior responds to changing conditions. One species of birds forages higher in the canopy than another. Conditions change: a storm brings down many trees. Behavior changes in response to the new conditions: the species that usually forages higher will move down. This changes the ecological interaction: competition between the 2 species increases.

There are countless examples of situations in which the ecological rules of engagement depend on behavior, so that when conditions shift, so does the ecological outcome. One set of examples arises when behavioral interactions lead history to determine community assembly (e.g., Blythe and Pineda 2009; Geange and Stier 2009). The same set of organisms do not always live in the same habitat, because history matters. The sequence in which certain species join the community plays a role in shaping distributions and abundances (Fukami 2010). As behavioral ecologists know, priority can determine resource use (e.g., Davies 1978). For example, Almany (2004) found that the order in which several fish species were recruited to a coral reef determined the distribution of species in the community, because the fish of some species did not stay if certain other species were there first. It is clear that history is important in the assembly of many communities, including those, such as protist or bacterial communities

(Fukami and Morin 2003; Price and Morin 2004), for which behavioral studies are in their infancy.

That behavior produces context-dependent ecological outcomes is recognized in the study of trait-mediated interactions, for example, of predator–prey interactions. When prey avoid a predator in one habitat but not in another, or prey respond differently to different predators, indirect interactions differ in outcome (Peacor and Werner 2000; Abrams 2005, 2007). For example, spider predators differ in behavior; some sit and wait for prey, but others actively hunt the prey. The grasshoppers, who are prey for the spiders, continue to forage when sit-and-wait spiders are nearby but are more likely to leave vegetation occupied by hunting spiders, with the result that hunting spiders decrease herbivory by grasshoppers more than sit-and-wait spiders (Schmitz and Suttle 2001). Behavior has been shown to influence many other indirect effects. Pollinators move away from crab spiders, and this can have drastic effects on seed set and fruit production in the plants that depend on those pollinators (Goncales Souza et al. 2008).

Another area of ecology for which behavior is important is conservation biology. Conservation biology is dedicated to the study of context-dependent ecological outcomes because it examines the effects of human disturbance. To make management decisions, we need to know how behavioral response to disturbance will affect population growth (Sutherland 2006; Caro 2007). For example, studies by Renton and colleagues on the lilac-crowned parrot in the tropical dry forest in Mexico (Renton 2001; Monterrubio et al. 2009; Salinas-Melgoza et al. 2009) show how nest choice depends on food availability, how dispersal distances and fledgling survival depend on nest choice, and how all these differ in the wet and dry seasons and in deciduous and semideciduous forests. Thus, the nesting and foraging behavior of the parrots links habitat availability to population growth. Understanding this behavior makes it possible to evaluate whether a particular reserve will sustain a population.

## BEHAVIOR AND THE ILLUSION OF ERGODICITY IN ECOLOGY

Ecology often represents ecological processes in terms of the functional relation among average values. For example, to ask whether an invasion will be more successful when there are many species in a community is to ask how an average propagule will fare when the average population sizes of many local species are high. Methods for evaluating ecological outcomes often assume ergodicity, that all samples are homogenous, and that the population being sampled is invariant. This can be misleading. Behavior is a response to conditions, but individuals vary in response, and conditions change. The result is that ecological processes are not ergodic: samples are not homogenous and processes change over time.

For example, average values, or “dominance hierarchies,” do not reflect the outcome of competition for food among ant species, because the outcome depends on behavior. When bait is offered to ants, some species are more likely than others to get it. But this is context dependent. Even within a particular community of ant species, which species dominate the bait varies in time and space (Sanders and Gordon 2003). Ant foraging behavior depends on local conditions, so that which species gets to the bait first and how persistent they are at fending off other species will affect the outcome. One example is the relation of the invasive Argentine ants and native species in northern California. In a northern California ant assemblage, all species, including the invasive Argentine ant and many native species, are likely to retreat from a food resource if another species is already there (Human and Gordon 1998). It seems that Argentine ants often get there

first (Gordon 1995), and this can tip the balance toward them in competition with native ants. Another example is from woodland ant species in the southwestern United States. Some species are hosts to a parasitic phorid fly. One of the host species is quickest to discover new resources because of its searching behavior. But when the flies are present, ants of the quicker species are less likely than those of other, slower species to capture food sources, because the foragers of the quick species stay away to avoid the flies (LeBrun and Feener 2007). The competitive interactions among ants are mediated by differences among species in their behavioral responses to phorid flies.

## THE FUSION OF BEHAVIOR ECOLOGY AND ECOLOGY

Questions about behavior lead to questions about ecology. I look out the window and see birds arrive in the top of an old live oak tree. First come a group of chickadees, then some warblers, and then juncos. Why do birds forage alongside birds of other species? Two possibilities familiar to behavioral ecologists are that one species signals to another the presence of food or that groups dilute the effect of predators. To learn whether it matters to birds that they are in the same tree, we need to know how the species overlap in the food they consume, how much predation occurs, and how the numbers in a tree affect the behavior of the birds and their predators.

There are many studies of mixed flocks that use the ecologists’ method, counts made by sampling birds at a fixed location (e.g., Hart and Freed 2003), to provide average numbers and composition of flocks. This method does not tell us how the samples reflect the context dependence of the birds’ behavior, so, although it is a lot of work to get the average values, even more work is needed to answer an evolutionary question about what it is that foraging together does for the birds. There are patterns in the lives of individuals, so that they tend to be in certain locations at certain times, and these patterns shift when conditions change, and the rules for how these patterns shift vary among species. It is the outcome of all these rules for where to go when, in which conditions, that lead to the presence of some towhees and some waxwings, right now, in the tree outside my window. To find out how foraging with other species affects reproductive success, we would have to ask, Where did the birds in that tree come from and where are they going? How often do these towhees end up in the same tree with those waxwings? How do birds vary in their responses to the factors that determine where they go, when? Learning about these patterns is a first step to understanding how the patterns are context dependent, that is, how the movement of birds adjusts to changes in the distribution and availability of food and the behavior of predators adjusts to the location of the birds. These rules of engagement determine how flocking affects food consumption, predator avoidance, and reproductive success.

Here is one more example, from my own work. Harvester ant colonies interact frequently with each other, but outright conflict is rare. Neighboring colonies compete for food (Gordon and Kulig 1996). Harvester ants eat seeds that are scattered by wind and flooding in ephemeral patches (Gordon 1993). Colonies forage in streams of ants, sometimes following trails cleared in the grass by the ants, or borrowed from neighboring kangaroo rats (Gordon 1995).

The more food is available, the longer the trails and the more likely are the trails of neighboring colonies to overlap, so that both are using the same area to search for seeds. The length of trails is linked to the current availability of food. Each forager leaves the trail to search for food, and then when it finds food, goes back to the nest. A forager goes back to the same location many times during a day (Beverly et al. 2009).

Each new forager moves past the ants on the trail closer to the nest, so the trail extends during the day as more foragers emerge (Gordon 1991). The more food is available, the more quickly ants find food, and the more ants forage because ants are stimulated to forage by other ants returning with food (Gordon et al. 2008). Thus, more food leads to more foragers and longer trails.

Whether a colony's trails meet those of its neighbors and what happens when they do, both change as a colony grows older. Colonies live for 25 years and begin to reproduce when they reach a mature size of about 10 000 ants at the age of 5 years (Gordon 1992). When the trails of mature colonies meet, those 2 particular trails are unlikely to be used the next day, so those 2 colonies avoid meeting in that place. However, a colony can have many trails in different directions, each headed toward a different neighbor, and one of a colony's trails meets one of a neighbors often, almost every day (Gordon and Kulig 1996). A system of patrollers that choose the day's foraging directions early in the morning (Greene and Gordon 2007) seems to help colonies avoid meeting the same neighbor at the same place day after day. Mature colonies are more likely to avoid conflict, whereas younger colonies, just before reproductive age, are more likely to return day after day to the site of conflict, even if this entails fighting (Gordon 1992). The foraging system, age structure of a population of colonies, neighborhood density, and the effects of weather on food availability all contribute to the ecological outcome of intraspecific competition for food. How natural selection might be shaping interactions between colonies (Adler and Gordon 2003) depends on these ecological processes.

#### WHERE DO WE GO FROM HERE?

Any behavior is part of a pattern that produces the ecology of the animal, so that ecological outcomes arise from behavioral processes. Behavioral ecology needs ecology to ask evolutionary questions because evolution depends on ecological processes. Ecology needs behavior to understand why outcomes are context dependent.

These ideas are obvious in principle but not often incorporated into the practice of behavioral ecology. Behavioral ecology sometimes views ecology as outside the domain of interest as if ecological processes merely set the stage in which the true behavioral drama unfolds. This is a mistake; behavior produces and modifies the ecological setting, so that the relation of behavior and environment goes both ways (Lewontin 2000; Kokko and Lopez-Sepulcre 2007; Laland and Sterelny 2008; Duckworth 2009), and ecological processes determine the evolution of behavior.

Context dependence requires us to redefine the project of relating behavior and fitness. It is not realistic to hope to find a reason why any trait would always be adaptive. Any trait, behavioral or otherwise, is deeply linked to others, genetically, developmentally, and functionally (Fodor and Piattelli-Palmerini 2010), and so no trait has ecological impact independently of all others. Moreover, even if we can ascertain that variation in certain behavior is associated with variation in reproductive success, changing conditions will still shift around that relation. Adaptive landscapes are full of small bumps, and the behavior itself modifies the landscape. If we watch long and carefully enough, we will see different consequences for reproductive success of the same behavior. The project, then, is to learn how conditions determine the ways that behavior contributes to variation in reproductive success.

Ecologists have come further in understanding the importance of behavior to ecology than behavioral ecologists have come in seeing the importance of ecology to evolutionary ques-

tions about behavior. Ecological journals are more likely to take articles that consider behavior than are behavioral ecology journals to take articles that consider ecology. *Ecology* has devoted special issues to topics in behavior such as trait-mediated interactions; *Oecologia* includes "behavioral ecology" as a category in a list that ranges from physiological to global ecology. By contrast, it is rare for behavioral ecology journals to publish work showing how ecological factors shape the consequences of behavior for reproductive success. It is time to recognize that behavioral ecology and ecology are not really distinct and to fuse behavioral ecology and ecology.

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