

Predation and competition: the interaction of two types of species interactions

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A perennial endeavor in community ecology is to unravel the relative importance of competition and predation in determining the structure of natural communities. The comparison stems in part from the suggestion that predation affects communities largely through its effects on densities of competing prey species (e.g., Jeffries and Lawton 1984) and that competition is important only when predation is weak (e.g., Connell 1975). We suggest that this comparison is misdirected. As we discuss here, predation and competition together can affect prey communities in a multitude of ways that often interact; appreciating the manifold complexities and consequences of this interaction of interactions may prove to be more fruitful than searching for which factor is "most important" in structuring ecological communities.

In this essay, we propose a simple classification of the effects of predation upon the outcome of competition. The basic idea is to distinguish between those effects that are mediated directly or indirectly through changes in prey population densities brought about by predator-inflicted mortality (trophic - link indirect effect, sensu Miller and Kerfoot 1987), and those mediated through changes in prey behavior which affect the intensity of competition among the prey species and are brought about in response to changes in the risk of predation (behavioral indirect effect, sensu Miller and Kerfoot 1987). We briefly discuss some of the diverse outcomes to be expected in systems with a mixture of predation and competition, and for illustration, relate theoretical models to a few examples from natural communities.

We present the following models as a convenient way for clearly categorizing the interaction of predation and competition. We present no analysis here, since much of that has already been done elsewhere.

One can represent the interaction between a pair of competing species with the following pair of differential equations:

$$\frac{1}{R_i} \frac{dR_i}{dt} = F_i(R_1, R_2) \quad i=1,2$$

where R_i = density of competitor i , and F_i = per capita growth rate function of competitor i . We assume that

the intensity of competition $F_i/R_j G_{ij}(R_1, R_2) < 0$ ($i, j = 1, 2$), so there is a negative density dependence both within and between species. The G_{ij} functions measure the marginal effect on fitness of additional competitors to the system. The general structure of the model can represent both interference and exploitative competition (Schoener 1976) provided resource densities equilibrate rapidly to changes in consumer densities. The conditions for stable coexistence in this model are well known (e.g., Maynard-Smith 1978, Holt 1985): each species must limit its own growth more than it does that of its competitor.

Predators can affect competitive interaction in two conceptually distinct ways. The first, which we call *density-mediated*, is through changes in competitor densities (and implicitly in resource levels) via an increase in mortality rates. This can be modeled as follows:

$$\frac{1}{R_i} \frac{dR_i}{dt} = F_i(R_1, R_2) - a_i(R_1, R_2, P)P \quad (1)$$

where P = predator density and $a_i(R_1, R_2, P)$ is the per capita, per-predator rate of consumption of prey i by the predator. In effect, an additional mortality term is tacked onto the competition equations given above, with no change in the pre-existing competitive terms at all. The intensity of competition in this model (as gauged by G_{ij}) is independent of predation. The total effect of one competitor on the other, of course, may depend on predation and has been termed "apparent competition" (Holt 1977) (see below).

We can contrast this to *behaviorally-mediated* effects of predation, which can be modeled as follows:

$$\frac{1}{R_i} \frac{dR_i}{dt} = F'_i(R_1, R_2, P) - a_i(R_1, R_2, P)P \quad (2)$$

where $F'_i(R_1, R_2, P) > (F_i(R_1, R_2))$ (unless $P = 0$). Here,

$$F_i/R_j = G_{ij}(R_1, R_2, P).$$

In addition to the direct effects of mortality on competi-

tion (i.e., the presence of P in the term furthest to the right of (1) and (2)), the predator influences the character of the competitive interaction itself (i.e., the presence of P in F_i of the left hand term of Eq. (2)). In contrast to the previous model, this one allows for prey to alter their behavior (e.g., diet choice, habitat, use, etc.) in response to predatory risk, and thereby, alter the competition term. In model (1), predation influences competitive interactions via the effect of mortality on prey growth rates; in model (2), predation also influences competitive interactions via the effect of predatory risk on the prey species' competitive term. We next discuss the consequences of predation acting on competition for each model, starting with model (1).

Most of the ecological literature on the effects of predation on competitive coexistence has implicitly or explicitly assumed model (1) (e.g., Holt 1977, 1984, Abrams 1977, 1987, Noy-Meir 1981). As discussed in detail elsewhere (Holt 1977, 1984, in press, Holt and Kotler 1987) a predator's numerical response generates an indirect interaction among alternative prey species whether or not they are competing for resources. Typically, this interaction is $(-, -)$ in character (i.e., apparent competition), so each prey suffers a reduction in density because of the presence of an alternative prey type in the predator's diet. If the predator does not show a numerical response, prey interact via the predator's functional response alone, often in a $(-, -)$ fashion. However, a $(+, +)$ interaction among prey is possible if the predator easily satiates or shows switching behavior since more time spent by the predator (whose total numbers and foraging time are more or less fixed) eating one prey species means less time spent eating the other (Holt 1977, Noy-Meir 1981, Abrams 1987).

To elucidate the effect of predation upon competitive coexistence, one must specify certain properties of the growth functions, F_i . In the simplest case of Lotka-Volterra dynamics in which predators have (to a reasonable approximation) linear functional responses to each prey, predation promotes coexistence only if the species which tends to be competitively excluded is better able to withstand predation (either because it has a higher intrinsic rate of growth or is captured less effectively; Noy-Meir 1981). In the linear model, predation does not alter the conditions for coexistence provided prey have equal intrinsic growth rates and are equally consumed (on a per capita basis) by the predator. However, this need not be true if the per capita effects of competition are nonlinear functions of density. Also, Abrams (1987) discusses a variety of effects of predation on a competitive system where the functional response is non-linear and outcomes range from $(-, -)$ to $(+, +)$. Holt (1985) discusses theoretical examples in which indiscriminate predation upon competitors with equal intrinsic growth rates enhances coexistence, along with examples of the opposite effect. The expected outcome hinges in a detailed fashion on how interspecific and intraspecific density-dependence vary with density.

A mechanistic basis for how a change in prey density due to predation can change the intensity of competition was suggested by Glasser (1979). As prey densities decline due to predation, the standing crop of resources which they exploit should become more abundant. For prey which are optimizing their diets, greater standing crops of the preferred food items will lead to greater diet specialization on the part of each prey species (e.g., MacArthur and Pianka 1966, Emlen 1966, Schoener 1971). If the coexisting prey species differ in what their most preferred food items are, then the change in prey density caused by predation will lead to a reduction in diet overlap and a reduced magnitude of per capita species interactions (i.e., F_i is a function of R_1 and R_2) (Glasser 1979). This would enhance the likelihood of prey coexistence. By contrast, if prey species share their preferred prey but differ in their less preferred prey, dietary overlap increases with the intensity of predation. This can make coexistence more difficult.

In contrast to model (1), which has received considerable attention in the ecological literature, the possibilities inherent in model (2) have barely been explored. Here, we will sketch some potential ways that changes in prey behavior due to predatory risk and the very presence of predators can influence competitive interactions. Here we consider two broad categories: 1) expected changes in homogeneous environments, and 2) shifts in habitat utilization in heterogeneous environments.

One general rule should govern how model (2) differs from model (1): prey species in model (2) are always affected by an additional evolutionary variable. If changes in prey behavior are adaptive, then animals which modify their behavior because a predator is present should have a higher per capita growth rate than those which do not modify their behavior. Such changes in behavior might then be reflected in altered population dynamics. Predation can directly affect competitive interactions if different prey activities have different associated risks. Foraging behavior especially may shift because of predatory risk. We will limit our discussion to the effect of predatory risk on foraging behavior, but other behaviors could be affected as well.

Throughout the rest of this note, we will assume that a species is comprised of individuals each of which use the same strategy (i.e., a single phenotype), the Evolutionary Stable Foraging Strategy, ESFS (Holt and Kotler 1987). Different species may use different strategies. Thus, when we note that a species changes its foraging behavior in a particular manner, we are actually referring to the individuals of that species using the ESFS characteristic of that particular species.

Consider the effect of predatory risk on prey foraging behavior in a spatially homogeneous environment. For instance, the risk of predation may cause foragers to move more slowly (Sih 1984, 1987, Abrams 1984). If the superior competitor is more vulnerable to predation than the inferior competitor, predation may increase

the likelihood of prey coexistence provided the inferior competitor can maintain its rate of food intake. The presence of the predator will decrease movement and feeding of the superior competitor and increase food availability for the inferior competitor. What happens if the rate of foraging is decreased equitably for two prey species because of the presence of a predator? This reduces the rate at which resources are cropped and therefore reduces the absolute magnitude of resource depletion caused by a given number of competitors. This does not necessarily imply that prey coexistence is more likely (Abrams 1977). However, the change in foraging rates as a secondary effect may alter dietary overlap. Consider a system of two competing prey species feeding on two or more resource types. In the standard model for optimal diet choice, a less preferred resource type is excluded from the diet if the preferred resource is encountered with sufficient frequency. If the two species prefer different resource types, but overlap in their use of a less preferred resource type, then a decrease in encounter rate because of predatory risk could lead to increased dietary overlap; thus, the presence of a predator may intensify competition. This effect may work in opposition to that predicted by Glasser (1979), which was based on changes in consumer density which resulted in changes in consumer behavior. We should note that if the prey have shared preferences for their most preferred resource type, but utilize distinct, less preferred types, then Glasser's effect should be reinforced. The same also holds for prey species exploiting depletable resources provided that the effect of increased predatory risk is to decrease foraging time (W. A. Mitchell, pers. comm.).

Predators can also influence how their prey select habitats and utilize a patchy environment. Consider a situation where predation is equal across all patches, but where, in the absence of predation, prey species value patches differently. Increasing predation will decrease the absolute values of all patches and may cause each prey species to stop visiting its least valuable patch type. When patch preferences are distinct (*sensu* Rosenzweig 1981), each species will drop a different set of patches from its foraging itinerary. Thus, more intense predation should lead to greater patch specialization (e.g., MacArthur and Pianka 1966, Schoener 1971) and more segregation of prey species by patch type (Sih 1987). Providing that the prey can withstand the intensity of predation in their most preferred patch types, this should increase the likelihood of coexistence. In essence, habitat partitioning becomes increasingly pronounced with increased predation. Conversely, shared patch preferences can lead to an increase in habitat overlap and thus an increase in competition.

Variability in rates of predation among patches may also influence prey interactions. Consider an environment with two patch types, a risky one and a refuge, and two prey species, one of which is more vulnerable to predators. Coexistence is promoted provided each spe-

cies has a habitat in which it is most efficient, even if both species do best in the same patch type in the absence of the predator (J. S. Brown, unpubl.). Habitat segregation may develop. The less vulnerable species may be able to exploit resources in the risky patch type that are largely unavailable to the more vulnerable prey competitor. If the more vulnerable species is the superior competitor in the safer patch type, habitat segregation may be observed. Habitat segregation comes about because the foraging activity of the more vulnerable but superior competitor excludes the less vulnerable species from the less risky patch type, while risk of predation along with the foraging activity of the less vulnerable species excludes the more vulnerable species from the risky patch. However, under extremely high levels of predation, this pattern may change, and both prey species may be restricted to the refuge. If so, predation leads to increased competition (e.g., Mittelbach and Chesson 1987).

Even if no habitat segregation occurs, coexistence of competitors in a patchy environment can be promoted by behavioral responses to predation provided individuals cannot do all of their foraging in a single patch and so must move from patch to patch. Coexistence is made more likely if the more vulnerable species in moving among patches is also a more efficient forager within patches (i.e., needs a less dense resource base in order to maintain itself). This mechanism can also promote coexistence when animals cannot respond behaviorally to predatory risk (J. S. Brown, unpubl.).

We have outlined several ways in which predation and competition can interact to structure biological communities which fall into two broad categories: density mediated responses to predator induced mortality (model 1) and behaviorally mediated responses to predatory risk (model 2). The two models may correspond to different kinds of natural communities. For example, competition for space among sessile organisms should almost always be characterized by model 1. Organisms which compete for space occupy a parcel of space more or less exclusively. The mechanism of competition exerted by an individual is to prevent the establishment of other individuals, or to prevent growth and encroachment by neighboring individuals. The intensity of competition will be a function only of the amount of space already occupied and the identity of the occupants, not predator density or predatory risk; predators only modify the amount of space available for establishment and growth or determine the identity of neighbors via selective predation. Examples include communities of sessile invertebrates and plants in the rocky marine intertidal zone (e.g., Paine 1966, 1974, Dungan 1987), and herbaceous plants subjected to grazing (Harper 1969). Preference by predators for the dominant competitor can at times increase species diversity; conversely, preference for poor competitors can increase the rate of competitive exclusion (e.g., Lubchenco 1978, Menge and Lubchenco 1981).

When organisms compete for food rather than space, model (2) is more apt to apply. This is especially true for mobile animals in spatially heterogeneous environments which can make choices regarding their use of habitats, microhabitats, and patches. In these cases, the most important effect of predation may not be the mortality it inflicts on prey populations, but rather its effect on prey behavior (e.g., Brown et al. 1988). For instance, the presence of predators can change the cost associated with foraging in particular microhabitats or performing certain activities. This can change microhabitat use, length of patch occupancy, and the total time spent foraging. Examples include instances where predation restricts habitat use, which can intensify competition, as well as those where spatial variance in predation promotes microhabitat partitioning. In an example of the first case, Gilliam and Fraser (1987) demonstrated a trade-off between foraging and mortality rates for stream fish such that fish choose patches with the highest ratio of energy intake to mortality rate. The authors note that when two species are subjected to similar risks from predators, avoidance of the most risky patches by both species may intensify the competitive interaction between them. This is seen in competing species of sunfishes in lakes where age-specific risk of predation restricts juveniles to the same habitat where they compete intensely and influence the number of each competing species (Mittelbach and Chesson 1987). As an example of the second case, spatial variance in the risk of predation appears to have led to microhabitat partitioning among coexisting granivorous desert rodent species in many communities in North America. The animals are found in simple habitats comprised of open and shrub microhabitats which differ in the risk of predation experienced by rodents. In addition, the rodents themselves differ in vulnerability to predators (Kotler et al. 1988). Species use the risky microhabitat in accord with their ability to detect predators (Kotler 1984). Here, predatory risk appears to provide an axis along which microhabitat partitioning can occur based on trade-offs involving predator avoidance and competitive abilities.

We should note that mobile, food-limited animals found in spatially homogeneous environments may sometimes more closely fit model (1). For example, Morin (1983) examined the effects of predation on competitive interactions, growth, and metamorphosis of six species in anuran tadpoles. Predation seemed to affect these quantities primarily through its effect on competitor density. Furthermore, two species of salamanders in the same system prey on microcrustaceans. Salamander predation facilitates small species by selectively removing highly competitive, large sized species (Morin 1987).

In summary, the ways in which predation and competition can interact to structure prey communities are manifold, but can be categorized into cases where effects of predation are indirect consequences of shifts in population densities and cases where predatory risk directly affects the magnitude of per capita competition

via changes in behavior. For organisms competing for space or for food in a homogeneous habitat, the effects may most often be felt through the reduction of competitor densities. Each individual of the competing species may still have the same marginal effect on the growth rate of individuals of the other species. There are just fewer of them. Consequences for prey coexistence depend on predator selectivity and the details of intra- and interspecific density dependence. For organisms competing for food in a heterogeneous habitat, however, the presence of a predator should often cause a change in the foraging behavior of the prey which alters the magnitude of per capita competition *per se*. In this case, predatory risk may alter habitat selection and modify the tendency for competitive coexistence.

In this essay, we have not tried to present a comprehensive classification of the ways that competition and predation may interact to structure communities. We only hope to convey that there are many ways in which they can do so, each with its special consequences. Rather than asking which is more important, competition or predation, we should focus on the ways they interact, for they are often inextricably linked in determining community structure.

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