

REVIEW

The interaction between predation and competition: a review and synthesis

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Abstract

This review discusses the interface between two of the most important types of interactions between species, interspecific competition and predation. Predation has been claimed to increase, decrease, or have little effect on, the strength, impact or importance of interspecific competition. There is confusion about both the meaning of these terms and the likelihood of, and conditions required for, each of these outcomes. In this article we distinguish among three measures of the influence of predation on competitive outcomes: short-term per capita consumption or growth rates, long-term changes in density, and the probability of competitive coexistence. We then outline various theoretical mechanisms that can lead to qualitatively distinct effects of predators. The qualitative effect of predators can depend both on the mechanism of competition and on the definition of competitive strength/impact. In assessing the empirical literature, we ask: (1) What definitions of competitive strength/impact have been assumed? (2) Does strong evidence exist to support one or more of the possible mechanisms that can produce a given outcome? (3) Do biases in the choice of organism or manipulation exist, and are they likely to have influenced the conclusions reached? We conclude by discussing several unanswered questions, and espouse a stronger interchange between empirical and theoretical approaches to this important question.

Keywords

Coexistence, diversity, herbivory, interaction strength, interspecific competition, predation.

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INTRODUCTION

Interspecific competition between species, defined as reciprocal negative effects of one species on another (either directly or indirectly mediated by changes in resource availability), has long been thought to be one of the more important processes determining the structure of natural communities (Cody & Diamond 1975; Diamond & Case 1986; Morin 1999). There is little doubt that

interspecific competition occurs in natural communities (Connell 1983; Schoener 1983; Gurevitch *et al.* 1992; Denno *et al.* 1995; Grover 1997). However, there is still uncertainty about the biological circumstances under which competition between species has a greater or lesser influence on the characteristics of species, their population densities and overall community structure (Chesson & Huntley 1997; Gurevitch *et al.* 2000). Predation is one of the factors believed to have a major impact on competitive

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interactions, and this article deals with the effects of predators on competition between prey species. We will consider predators to include any organism that has a negative effect on the immediate per capita population growth rate of a prey species by consuming part or all of prey individuals (e.g. herbivores, parasites).

The current range of views on the interaction between predation and interspecific competition appears to present a confusing picture. Experiments designed to determine the effect of predators on competition between their prey have resulted in almost every conceivable outcome: sometime predators have been shown to increase the strength of interspecific competition or its impact on a prey community; sometimes predators have been shown to decrease competitive strength or impact, and in yet other cases, predation has very little effect on competitive interactions. There are also cases in which different intensities of predation have had qualitatively different effects on competition. Usually there are several potential explanations for each of the qualitatively different effects of predators on competitive interactions between prey species, but seldom has one particular explanation been shown to be overwhelmingly more likely than any of the others.

We will argue that this appearance of confusion is at least partially misleading. Theory has identified a variety of mechanisms for each of the qualitatively different effects that have been observed. Most, if not all, experimental observations are consistent with this body of theory. In at least some cases, one particular mechanism seems most likely to have caused the observed effect. In many other cases, we do not have enough information to clearly establish which of several possible mechanisms is responsible for the observed effect. We feel that progress in understanding the interaction between these two interspecific interactions will be facilitated by: (1) greater clarity in defining what is meant by the “strength”, “intensity”, “impact” or “importance” of competition; (2) greater attention to distinguishing between different mechanisms by which predation alters interspecific competition between prey species; and (3) greater recognition of potential biases in the systems selected for study and the organisms selected for manipulation. It has been more than 15 years since Yodzis (1986) presented a combined review of theory and empirical work dealing with the interaction of predation and competition. This article will attempt to provide an update on the state of our knowledge of this important topic.

We begin by discussing various possible definitions of the strength of interspecific competition. This is followed by a summary of current theory regarding the possible effects of predation for each of these definitions. We couple this with a selective review of empirical work to see to what extent

empirical studies illustrate or can be explained by current theory. We also ask to what extent previous empirical work can form a basis for generalizations about relative frequencies of different types of effects of predation on competition. The final section suggests ways to advance our understanding of the interaction between predation and competition in both theoretical analyses and empirical studies.

HOW DIFFERENT MEASURES OF COMPETITION CHANGE UNDER THE IMPACT OF PREDATION: DEFINITIONS, THEORY AND DATA

Qualities such as “strength”, “intensity”, “impact” and “importance” are frequently not defined when they are applied in discussions of interspecific competition, or how it is altered by predation. For example, in a recent meta-analysis and review paper Gurevitch *et al.* (2000, p. 445) concluded that “In general, predation may act to reduce the intensity of competitive interactions”. Although stated in general terms, this conclusion is sensitive to the definition of “intensity”, as we discuss below. In practice, definitions of the effects of interspecific competition have typically fallen into one of three categories: (1) reduction in the average resource intake rate (or some resource-determined component of fitness) of individuals of one species caused by the presence of the competing population; (2) absolute or proportional reduction in population density caused by the presence of a competitor, assuming that coexistence occurs; (3) probability or frequency of competitive exclusion or coexistence among species (including measures of species diversity). Distinguishing the measure being used is crucial, because each of these measures can be affected quite differently by predation.

Below, we discuss how predators affect each of the three measures of interspecific competition. The text is summarized in Table 1, which presents a synopsis of the types of effects that are expected when predators are added to a competitive system, together with the biological conditions when those effects are likely to occur. We discuss the theoretical basis of this table by considering each of the three measures of competitive intensity below.

Measure 1. The impact of a competing prey population on the *per capita* resource intake rate or growth rate of a focal prey species

It is often necessary to consider three trophic levels in analysing the effects of predators on competing prey. The resources that support prey populations are usually important determinants of the effects of predators. Here,

Table 1 Theoretical predictions regarding the effect of predators on the intensity of competition

Measure of competition	Possible effects of predation on the measure
Reduction in resource intake (or individual growth)	<ol style="list-style-type: none"> 1. Predation generally reduces competition if measured by the total effect of the competitor population. 2. Predation may increase or decrease competition if measured by the average effect of one individual.
Reduction in density caused by a competitor population	<ol style="list-style-type: none"> 1. The absolute reduction in population size caused by a competitor is usually reduced by predation, but the proportional effect may increase or decrease. 2. Proportional effects of a competitor on equilibrium abundance are usually changed by predation in a manner similar to changes in the ease of coexistence.
Ease of coexistence (range of parameter values producing coexistence of competitors)	<ol style="list-style-type: none"> 1. If predators generate resources, increase resource diversity or add limiting factors, they favour coexistence. Promotion of coexistence is especially likely if the prey species compete for space, are very efficient consumers of their own resources, are consumed by an array of specialist predators, or show a trade-off in competitive ability versus predator defence. 2. High enough predation can make prey species sensitive to even a small amount of competition, and thus promote exclusion. 3. Selective predation on dominant competitors can increase prey diversity when the other competitors are capable of coexistence. 4. Behavioural shifts in relative resource utilization rates of prey in response to predation may have a variety of effects on ease of coexistence.

and in the following sections, we use “consumer” and “prey” interchangeably to mean the middle (competing) level in these three-level systems; “predators” refer to the top level. Addition of predators (or other mortality sources affecting consumers) usually reduces the population size of the consumers (Sih *et al.* 1985). This lower consumer density then allows resources to increase. Thus, the decrease in resource densities brought about by a competing consumer will usually be smaller if the competitor population is kept at a lower density by the predators. The same would be true of any other factor that reduced the densities of the competing consumer. If the intensity of competition is measured in a currency related to the effects of the entire competitor population on the absolute availability of shared resources (e.g. as the difference in individual growth rates of the focal species in the presence and absence of the competitor), this measure will usually be smaller in the presence of predators than in their absence. This generalization usually extends to the case of short-term (e.g. one generation or less) changes in population density caused by competition; such changes are usually smaller in absolute magnitude when predation reduces the maximum density that the competitor may attain. Of course, the preceding generalizations do have some exceptions. For example, if predation rates are relatively low, the main effect of the predator may be to induce habitat or behavioural shifts that can either strengthen or weaken one or both competitive effects between a pair of species (Peacor & Werner 2000).

While the absolute effect of a competitor population on the resource intake rate of members of a focal species is

likely to decline after predators have reduced competitor densities, the *per capita* effects may increase or decrease. This is because the size of the *per capita* effects in consumer-resource models of competition depends sensitively on the functional responses of the consumers and the growth functions of the resources (Abrams 1977, 1980). Similar effects of predation on competition apply when competition is via interference.

Empirical measures of these short-term effects arising from a single density manipulation can usually be made more easily than the longer-term effects discussed in the next two sections. Gurevitch *et al.* (2000) present a recent meta-analysis of studies, some of which addressed the effects of predators and competitors on short-term fitness components. Their measure of “competitive effect” was the absolute change in a performance measure (population size, individual growth rate, short-term change in population size, etc.) caused by the presence of a competing species. In general, they found good agreement with the expectation that in the presence of predators, the effects of interspecific competitors on measures of individual growth, fitness, or short-term population growth, were less than they were in the absence of predators (Gurevitch *et al.* 2000). P. Håmbäck and A. Beckerman (unpublished observations) present a similar review of studies focused more specifically on the effect of herbivory on plant competition. Although these results are consistent with theory, for many fitness measures there are statistical as well as biological causes underlying the observed effects. This is because a predator reduces the values of response variables in the absence of competition, and therefore it necessarily reduces the

maximum amount to which these fitness components can be further reduced by its competitor. In this case, an interaction between the two processes will be detected, even when this interaction is not biologically meaningful (e.g. Wootton 1994).

In summary, theory and experiment agree that the absolute effects of a competitor population on the fitness components of a focal species are usually lower when the focal species and competitor are both at lower population densities due to the presence of predators. Unfortunately, absolute effects measured on a short time-scale tell us little about the impact that predators might have on measures of interspecific competition over longer temporal scales. Such effects on equilibrium population size and coexistence are considered in the following two sections.

Measure 2. The change in the equilibrium or long-term average density of a focal species following competitor addition or removal

Changes in the density of a focal species following competitor manipulation may be considered over any time-scale and following any amount of change in competitor populations; different magnitudes of such manipulations may give qualitatively different answers (Bender *et al.* 1984; Abrams 1998, 2001b). However, what is usually of interest is a time-scale long enough for the system to approach some limiting dynamical behaviour, and a change equivalent to complete removal of the competitor. (Less extreme changes in density may also be of interest but have seldom been studied.) In addition, what is often of interest is the proportional (rather than absolute) change in density of a focal species caused by the addition or removal of a competitor. Clearly, an increase in predation, or any other source of mortality, will generally reduce the absolute change in consumer density when a competitor is added or removed, simply because the direct effect of predators is to reduce the density of their prey.

There is a surprising dearth of both theory and experiment on proportional change in equilibrium population size produced by competitors under different circumstances. Some special cases and particular models have been examined. If only the density of the focal species limits the predator, then the competitor will frequently have no impact on the density of the focal species, which will eventually come to rest at the density set by its predator's requirements. Abrams (1977) analysed a model of competition for abiotic resources in which increased mortality of each of two competitors increases the proportional reduction in one species caused by the addition of the second. In contrast, a model for competition between two consumer species for biotic resources (Abrams 1998) predicts that mortality imposed on both competitors can sometimes decrease the

proportional impact of each one on the density of the other. Although density changes have been studied in several of the short-term empirical studies reviewed by Gurevitch *et al.* (2000), short-term results cannot simply be extrapolated because almost all perturbations result in non-linear changes in population densities over time. Empirically, little is known about how predation affects long-term changes in density brought about by a competitor. In theory, this effect depends largely on how predators change the ratio of inter- to intraspecific competition. The following section defines this ratio and discusses how it influences the probability that species will coexist, and how it is likely to change under the impact of predation.

Measure 3. The probability of competitive exclusion or coexistence

Of all of the measures of competitive intensity, the probability of prey species coexistence has received the greatest amount of attention from theorists interested in determining the impacts of predation on competitive assemblages (e.g. Slobodkin 1961; Cramer & May 1971; Van Valen 1974; Abrams 1977, 2001a; Yodzis 1978, 1986; Noy-Meier 1981; Holt 1985; Kotler & Holt 1989; Holt *et al.* 1994; Chesson & Huntly 1997; Chesson 2000). Most of this work agrees that there is no generally applicable reason why simply reducing the densities of competitors should increase the range of other conditions over which they will coexist. Depending on both the nature of competition and of predation, predators can increase, decrease or have no effects on the probabilities that prey species can coexist. This diversity of predictions contrasts with the simple theoretical and empirical results regarding short-term impacts on fitness components (measure 1).

The diversity of potential effects of predators arises because coexistence depends primarily on the ratio of interspecific effects to intraspecific effects (Van Valen 1974; Abrams 1977; Holt 1985; Chesson & Huntly 1997; Chesson 2000), and this ratio has been shown to have a variety of responses to predation, depending on the details of the system. The centrality of this ratio to coexistence is implicit, for example in the textbook Lotka–Volterra model of interspecific competition, where coexistence is determined by the competition coefficients. These coefficients are simply ratios of *per capita* inter- to intraspecific effects of population size on *per capita* growth rate. Predation generally reduces both inter- and intraspecific effects, but in the absence of other complexities, need not alter their ratio (Abrams 1977; Holt 1985; Kotler & Holt 1989; Chesson & Huntly 1997). Figures 1 and 2 provide a simple graphical illustration of this result. They show how uniform mortality (which may be caused by a constant, non-selective predator population) alters the relationship between resource density

and competitive dominance under exploitative competition. Figure 1 shows how the *per capita* growth rates of two consumer species might change with the density of a single limiting resource. For a given mortality rate, only one consumer species (the one for which growth and mortality balance at the lower resource density) can persist when the system is at equilibrium. Adding a predator that imposes uniform mortality changes the intersections of the *per capita* growth and mortality curves. Thus, increased predation means that consumers require a greater resource density to balance their added mortality rates, and equilibrium resource levels will be higher. In this case, greater resource density may change the identity of the excluded species, but will not prevent exclusion from being the ultimate outcome. High enough mortality will preclude the existence of either species. Figure 2 considers the case with two limiting resources. With low mortality (predation) each consumer is potentially limited by a different resource and stable coexistence at equilibrium may be possible according to the rules of simple resource competition (e.g. MacArthur 1972; Grover 1997). However, in the example presented in Fig. 2, sufficiently high mortality will eliminate the possibility of coexistence entirely, because the same consumer species grows more rapidly on each of the two resources at high resource densities. Of course, other shapes of the consumers' growth curves may produce different outcomes, including the case where coexistence is impossible in the absence of predators, but may occur when predators are added (see below). Nevertheless, Figs 1 and 2 show that the higher resource levels that often result from higher levels of predation need not promote coexistence *per se*.

The general theoretical results reflected in these figures contradict the idea that simple reduction in the population sizes of competitors should necessarily promote coexistence (e.g. Connell 1971). Nevertheless, the idea espoused by Connell (1971) is still relatively common, as we discovered in an informal survey of colleagues, in a search of recently published literature, and in several general ecology textbooks. The popularity of these ideas may indicate that there are specific mechanisms of competition or predation that

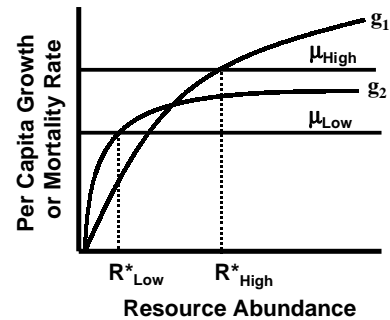


Figure 1 Simple depiction of the effects of increased mortality rate (e.g. due to predation) on the competitive interaction between two species that compete for a common resource. Growth curves for each species are depicted as g_1 and g_2 , respectively, and increase asymptotically with increasing resource supply. Mortality (μ) is constant (does not vary with resource abundance), and is low (μ_{Low}) when predators are absent and high (μ_{High}) when predators are present. Here, we assume that the mortality constant is identical for each species with and without predators. Where the growth curve for each species intersects the mortality constant gives the equilibrium level of resources expected (R^*), and the species that can reduce resources to the lowest level will win in competition and exist alone.

lead to this outcome and that apply to most communities. To determine whether this is true, we must look in more detail at the mechanisms by which predation may affect the ease of coexistence of competing prey species.

The following subsections explain most of the currently known mechanisms by which predators affect the ratio of inter- to intraspecific competition, and thereby, coexistence. Before considering these, it is important to note that predation (especially high levels of predation) must reduce the range of environments that allow a species to exist, even in the absence of competition. Some environments simply will not support sufficient reproduction to balance the mortality caused by the predator. Therefore, even if it has no effects on the ratio of inter- to intraspecific competition, predation is often expected to make coexistence more

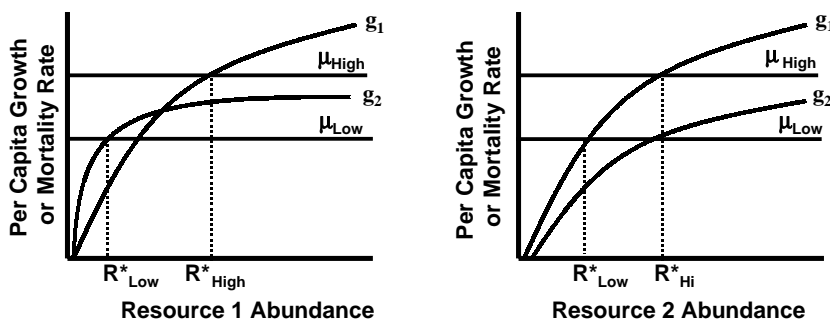


Figure 2 Similar to Fig. 1, except with two limiting resource types. The left panel represents the growth and mortality curves for two species on resource 1 (same as Fig. 1), while the right panel represents the growth and mortality curves on resource 2. See text for interpretation.

difficult by virtue of making existence more difficult. In addition, one or more of the following mechanisms may operate.

(a) Predators alter the diversity of the prey's resources

Predators can have significant effects on the diversity of their prey's resources, and thus on the potential for resource partitioning among competing prey. In the case of consumptive competition, efficient consumers of more than one resource species may drive some of those resources extinct, or to very low levels, via apparent competition (*sensu* Holt 1977; Abrams 2001a). Under these conditions, predation on the competing consumers can increase the probability of coexistence by increasing the diversity of resources that are able to persist, which allows between-consumer differences in resource utilization to be expressed. If consumer mortality due to predation increases further, predation has little effect on resource diversity simply because the already small consumer populations have little effect on resource abundance. In such a case, the negative effect of predation on existence will also lead to a negative effect on coexistence. This produces a predicted unimodal relationship between prey species diversity and intensity of predation.

The same sort of relationship is expected under space competition. Space competition is often hierarchical. Space occupied by one species may be taken over by members of other species having higher ranks in a competitive hierarchy. Resource items that are differentially available to different consumer species represent functionally distinct resources from the standpoint of coexistence theory (Abrams 1988), so that spaces occupied by differently ranked competitors represent functionally distinct resources. When prey species have an inverse ranking of dispersal and space-acquiring abilities, predation will have offsetting effects on prey diversity. Predation frees space, which increases the opportunity for succession from low- to high-ranked competitors, and thus increases resource diversity. This mechanism again leads to a predicted unimodal relationship between predation intensity and prey diversity (Levin & Paine 1974; Yodzis 1978). Further, this is true whether the competition is for space itself or is simply spatially localized competition for resources such as food. A similar mechanism may account for coexistence under other types of hierarchical competition, such as competition for light in a vertical gradient (Chesson & Pantastico-Caldas 1994).

A conceptually similar, but biologically distinct, way in which predators can alter the ratio between intra- and interspecific effects, and the conditions for prey species coexistence, is by altering the types of resources which are limiting. For example, predators often create a need for spatial refugia, where risk of being caught by the predator is

reduced or eliminated. Before the predator is added, such refugia may have no effect on prey fitness and therefore do not constitute resources (Abrams 1988). However, in the presence of the predator, they generally become resources for the prey species; i.e. factors that increase prey fitness, are in limited supply, and are consumed by being occupied. If different prey species have exclusive refugia, or differentially utilize refugia, then addition of the predator generates limitation of the prey community by multiple resources, and thereby promotes coexistence (Jeffries & Lawton 1984; Holt & Lawton 1994). On the other hand, if all prey must utilize the same refuge, addition of the predator may increase the mean amount of overlap in resource use, and cause a decrease in the diversity of prey species. Even in the absence of refuges in a strict sense, if different resources are associated with different risks of predation, then predators will often cause prey to alter their behaviour to avoid risky resources, which will alter the conditions for species coexistence, depending on whether risky resources are used by many or few species in the absence of predation (Kotler & Holt 1989).

(b) Predators alter conditions for coexistence by acting as limiting factors

Limiting factors impose higher mortality (or lower natality) as the population of the species being limited increases. As Levin (1970) showed, it is the number of limiting factors, rather than resources *per se*, that sets an upper limit to the number of competitor species at equilibrium, and it is overlap in limiting factors in this broader sense that determines the ease of coexistence. Because predator numbers and/or feeding rates often increase in response to abundant prey, predator species represent potential limiting factors. When the relative *per capita* predation rates on different prey do not change with prey densities, the predator represents a single limiting factor. Each predator species with a distinct set of relative consumption rates represents a different limiting factor. Technically, if the different predator species have sets of consumption rates that are linearly independent of each other, then there will be as many additional limiting factors as there are predator species (Levin 1970). In this case, different predators can respond differently to a given change in the prey community. A simple example occurs when each predator is specialized on a different prey species, and acts as a limiting factor for that prey (Janzen 1970; Grover 1994). In this way, predators add indirect intraspecific density dependence, thus increasing the ratio of intraspecific density dependence to interspecific density dependence, and promoting coexistence.

In another well-known example, a single generalist predator can allow coexistence of two prey that compete for a single food type, provided the species that is a better

food competitor is more affected by predation. This trade-off ensures that one species is limited primarily by the resource, and the other primarily by the predator (Armstrong 1979; Abrams 1993, 1999a; Holt *et al.* 1994; Leibold 1996). However, even this mechanism need not lead to coexistence among prey species, and only does so under limited environmental conditions (Holt *et al.* 1994; Leibold 1996; Grover & Holt 1998; Abrams 1999a; Chase 1999; Chase *et al.* 2000). If the predator is very efficient, then it may be much more important than the resource as a limiting factor, leading to exclusion by apparent competition (Armstrong 1979; Holt *et al.* 1994). Even specialist predators, each dependent on a different prey species, will not guarantee coexistence of competing prey unless the predators are all sufficiently efficient and are limited primarily by their prey (Grover 1994, 1995).

Coexistence of competing prey species can also occur if the *per capita* consumption rates of different prey species by a single generalized predator vary with prey density, and the predator exhibits switching behaviour (Murdoch 1969; Roughgarden & Feldman 1975). In this case, the predator disproportionately consumes whichever species is most common, allowing potential coexistence of any number of prey species. Switching can make one predator species effectively equivalent to any number of limiting factors. Optimal patch choice by predators can produce switching, and may therefore facilitate prey coexistence if different prey species use distinct microhabitats (Holt 1984; P. Hambäck and A. Beckerman unpublished observations). The same is true of optimal diet choice by predators in a fluctuating environment (Hambäck 1998). Predator switching behaviour need not be perfect to result in very high prey species diversity, although there are some limits on the effectiveness of switching when the behavioural change is not fast relative to population dynamics, and the prey undergo population cycles (Abrams 1999b).

When predators act as limiting factors, the interpretation of their effect on coexistence becomes problematic. Unless one includes apparent competition and other negative indirect effects in the definition of competition (which we have not done), increased competitive exclusion in the presence of a predator need not imply greater competition as measured by ratios of inter- to intraspecific effects on resources. In fact, exclusion may be more likely in the presence of a predator even though the ratio of inter- to intraspecific competition (using our narrow definition) is greatly reduced. We have ignored this complication here because previous experiments and observations generally do not permit determination of the cause of extinctions.

Each of the three mechanisms discussed above has the capability of either promoting or inhibiting coexistence. When assessing these mechanisms in the field, it is important to remember that predator preferences may lead

to effects on prey diversity that differ from the general predictions addressed above. If predators prefer to eat competitive dominants, they will increase the equality of competitive abilities, which promotes coexistence. However, when predation becomes intense enough that the former dominants are disadvantaged relative to other prey species, further increases in predation decrease diversity. For some intensities of predation, a predator preference for dominants will lead to increases in prey diversity even when one of more of the above mechanisms suggests that coexistence should be more difficult. Such effects have been discussed by many authors, including Slobodkin (1961), Holt (1985) and Chesson & Huntly (1997).

Although we have concentrated on exploitative competition in this section, interference mechanisms also lead to a range of possible impacts of predation on coexistence. Positive effects of predators on coexistence would require that they reduce interspecific interference more than intraspecific interference, and there does not appear to be any general reason why this should be the case more often than the reverse. In summary, the ease of coexistence among interspecific competitors is capable of changing in several different ways with the incidence or density of predators. What appears to be generally true, however, is that none of the various mechanisms discussed here provides a blanket justification for a belief that predators make coexistence of their prey species more likely. The next section will consider what empirical work has told us about the interaction of predation and competition.

Empirical evidence regarding the effect of predation on coexistence

The aggregate conclusion of simple models regarding coexistence – that predation or other sources of mortality can have positive, negative or no effect on coexistence – was borne out by the review by Yodzis (1986) of the empirical literature up to that point. This is not particularly surprising. More significantly, it is also true that most of the exceptions to the idea that predation promotes coexistence have occurred in systems where theory predicts that exceptions should be common: those with high intensities of predation, and with competition for resources other than space (e.g. Addicott 1974; Risch & Carroll 1982; Spiller & Schoener 1998).

Since Yodzis' (1986) review (see also Crawley 1983), the experimental evidence for an effect of predation on the number of coexisting species has continued to be mixed. There have been many studies in which the presence of predators increases the diversity of prey species. However, studies in other systems have found that predators reduce prey species diversity (see review by Proulx 1998 & Mazumder). For example, Spiller & Schoener (1988, 1998)

showed that predatory lizards greatly reduce the overall diversity of spider species on Bahamian islands by excluding rare species, and Augustine & McNaughton (1998) review several incidents where ungulate herbivory decreases plant species diversity in forests. Increased grazing can increase plant diversity with low initial herbivory, but decrease plant diversity when herbivory is still more intense (Lubchenco 1978; Sommer 1999). In all of these cases there are several potential mechanisms that might account for the decrease in diversity following increased predation, and the available empirical information generally cannot determine which, if any, contributes significantly to the observed changes in diversity.

Patterns that might reveal the mechanisms responsible for predator effects on prey competition are most likely to emerge from comparative analyses of several experimental studies. Proulx & Mazumder (1998) found an intriguing pattern in a recent analysis of the experimental effects of herbivores on plant species richness. Grazers decreased plant diversity in ecosystems that they characterized as low in productivity, but increased plant diversity in ecosystems characterized as high in productivity (see also Proulx *et al.* 1996; but see Buckland & Grime 2000 for a different pattern). This pattern suggests several potential mechanisms, including:

- 1 In low productivity environments, populations are too small to affect resource diversity, so predators simply reduce species number by reducing the range of conditions that allow existence. At high productivity, populations are large enough to depress one or more resources to low levels, and predators increase resource diversity or add to the number of effective limiting factors, increasing coexistence (and diversity) among prey species.
- 2 In low productivity environments, well-defended species cannot exist because they are poorer at sequestering resources, and consequently predation eliminates some of the vulnerable species. In high productivity environments, predation allows the persistence of inedible species, but is not sufficient to cause extinction of the vulnerable species because of their faster growth rates (Proulx & Mazumder 1998).
- 3 The correlation between traits that increase competitive ability and vulnerability to predation may be stronger, or even reversed, in productive relative to unproductive environments. This trade-off means that herbivores only increase plant diversity in more productive environments. For example, grazers may choose taller plants, which are also those superior at competing for light in high-productivity environments, and thus grazers would promote diversity. Alternatively, such differences in height would not be expressed strongly in low produc-

tivity environments, and grazers would not promote diversity.

The predatory impact on coexistence need not be identical for all groups within the prey community. Some experimental studies suggest that predators enhance the likelihood of coexistence among one subset of prey species, but reduce the likelihood of coexistence among other prey species. For example, Spiller & Schoener (1988, 1998) showed that the presence of insectivorous lizards had different effects on the species diversity of spiders that were initially rare and those that were initially abundant (see also e.g. Wootton 1995; Proulx *et al.* 1996; Augustine & McNaughton 1998). Because of the multiplicity of mechanisms by which predation can affect conditions for coexistence, the operation of one particular mechanism or the existence of one particular outcome (e.g. increased coexistence of a subset of prey species), can be obscured when considering a large heterogeneous group of species.

DISCUSSION

Predation may promote, hinder or have no effect on interspecific competitive interactions and the probability of prey coexistence, depending both on the mechanisms of predation and competition and the measures of interest. Historically, it has been suggested that if predators are important, competitors are less so. The continuing influence of this idea may have several roots. The first is the lack of definition of "intensity" or "strength" in many studies of competition. This fosters the belief that different measures of competition should be affected in similar ways by predation. It is certainly true that, when measured by absolute effects on fitness components in the short term, predation is generally predicted to reduce competition. Furthermore, this prediction is supported by experimental data (Gurevitch *et al.* 2000). However, this does not imply qualitatively similar effects on either long-term densities or the probability of coexistence.

There are long historical roots to the idea that predation uniformly reduces competition, going back at least to Hairston *et al.*'s (1960) famous hypothesis that predators and plants, but not herbivores, suffer extensive competition for resources (see Connell 1983; Schoener 1983; Sih *et al.* 1985; Gurevitch *et al.* 1992, 2000 for empirical reviews in this context). In addition, many of the early field experiments on competition seemed to support the idea. This includes Connell's (1961a,b) work on barnacles and predatory snails in Scotland, Paine's (1966) study of a variety of intertidal invertebrates and starfish predators off the Washington (USA) coast, and other studies such as Brooks & Dodson (1965), Hall *et al.* (1970) and Menge &

Sutherland (1976). The findings of these studies were most likely due to competition for space in hierarchical communities, and preferential predation on a competitive dominant. In these cases, the expectation is that predation will increase diversity until its intensity becomes high, but this is not because of an overall decrease in the competitive intensity of the prey species *per se*, but rather a shift in the *per capita* effects. In addition, and perhaps more problematic, was the fact that experimental studies, such as those in the intertidal, were inherently open systems, as recruitment was strongly influenced by processes outside of the experimental arena, whereas the theory typically considers closed communities (see below). Furthermore, most of the early studies did not examine a graded series of different intensities of predation, and thus could have missed part of the picture. Lubchenco (1978), who did study a gradient of predation intensity, observed the theoretically expected unimodal relationship between predation intensity and prey species diversity (see also Sommer 1999).

Some biases in the choices of experimental systems and types of manipulation

If we are to obtain a better understanding of when and why predation affects competition in particular ways, it will be important to consider biases in choices of experimental system and manipulation when interpreting reviews or meta-analyses. Bias can affect choice of study system. For example, space-limited communities are unusually conducive to long-term studies of competition. In generalizing from the many studies of predation in such communities, it should be recognized that their results apply best to similar systems with hierarchical space-related interactions. Osenberg *et al.* (1999) discuss such biases in choice of study system in more detail.

Biases may also arise from the type of manipulation carried out. Many field manipulations take place in experimentally closed systems, such as enclosures, in order to impose the appropriate treatments. Alternatively, experiments in open systems typically have very short time-scales of experiments, and are small relative to the surrounding unmanipulated area, and thus are strongly influenced by immigration from outside. In either case, species that are not present at the initiation of the experiment have difficulty entering the system. Thus, a manipulation will generally decrease, or leave unchanged, the number of species. This may introduce bias into experimental studies of the effects of predators on prey species coexistence and diversity. In effectively closed systems, both predator removal and predator addition are likely to reduce prey diversity, even if the diversity might increase in a more open system. If one of these two types of manipulation is more common, it is likely to bias any meta-analysis performed on the effect of

predation on prey species coexistence. For example, one of the clearest cases of predators reducing diversity comes from the experimental introductions of lizards onto islands (Spiller & Schoener 1988, 1998). In this case, predators caused the extinction of prey (spider species) that were already coexisting. Alternatively, one of the most well-known cases of predator-mediated coexistence comes from Paine's (1966) study, where he removed starfish from the intertidal and showed a consequent decrease in prey diversity. In both of these examples, prey species went extinct. However, the nature of the manipulation, due to predator addition or removal, led to a fundamentally different conclusion as to the effect of predators on prey species coexistence and diversity. At the same time, it is also important to realize that in some experimental situations, high enough levels of immigration will prevent exclusion, and species diversity could be largely determined by immigration from outside of the experimental arena, rather than local interactions alone (Loreau & Mouquet 1999).

Finally, biases may also occur with respect to the choice of which competitor to manipulate. For example, in several studies that simultaneously considered predation and competition (Gurevitch *et al.* 2000), only the superior competitor in a pair of competing species was manipulated. Thus only one of two competitive effects was measured, which may have biased the meta-analysis of these experiments towards finding a reduction in competitive intensity in the presence of predators. A long line of studies has found evidence of a trade-off between the abilities to compete for resources and resist predators (e.g. Lubchenco 1978; Lynch 1979; Grover 1995; Kraaijeveld & Godfray 1997; Bohannan & Lenski 2000; J. M. Chase, unpublished observations). If such a trade-off is as general as it seems, then the dominant resource competitor in the absence of predators will be greatly reduced by predation, and its measured "effect" on the subordinate species will be reduced. However, by the same token, the effects of subordinate competitors on the dominant, which often go unmeasured, would be likely to have increased in the presence of predators. For example, the data in Fig. 3 (from J. M. Chase, unpublished observations) show that when the presence of two freshwater snail species was reciprocally manipulated in the presence and absence of a predator, the competitive effect of each snail species shifted. While predators reduced the competitive effect of the superior resource competitor (*Physella*, which survived less well under predation) on the inferior, they increased the effect of the inferior resource competitor (the more predator-resistant *Helisoma*) on the superior. Bohannan & Lenski (2000) report similar results from a system of a bacteriophage and two bacterial strains competing in continuous culture for a limiting substrate. At low substrate supply rate, the competitive effect of the superior resource competitor on

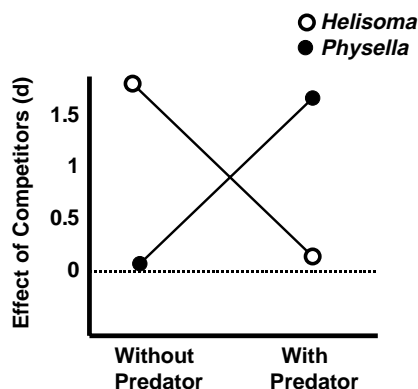


Figure 3 Results from a factorial experiment simultaneously removing the presence of a competitor and predator (*Belostoma flumineum*) for two common species of freshwater snails, *Physella* and *Helisoma* (J. M. Chase, unpublished data). Y-axis values are calculated from Gurevitch *et al.*'s (2000) formula for effect size (d), indicating the competitive effect on the species indicated imposed by the other species. Effect size was calculated from the biomass (g) of species in experimental enclosures with and without competitors and with and without predators. *Physella* is a superior competitor and excludes *Helisoma* in the absence of predators, and thus the relative effect of competitors on this species is very low without predators. *Helisoma* is more resistant to predators, however, and becomes the superior competitor with predators present, and thus the effect of competition on *Physella* dramatically increases when predators are present. The reverse result is true for the relative effects of competition on *Helisoma* biomass with and without predators. Combined, these results show that the effect of predation on the intensity of competition depends on which species is being manipulated.

the inferior was greatly reduced in the presence of the phage. In contrast, the inferior resource competitor only had a measurable effect on the population size of the superior resource competitor when the phage was present.

The bias in favour of manipulating competitive dominants may have played a previously unnoticed historical role in the conceptualization of interactions between predation and interspecific competition. In his classical experiment, Connell (1961a,b) manipulated the presence and absence of a predator (*Thais* [= *Nucella*]) and an interspecific competitor (*Balanus*) to determine their effects on the distribution of an intertidal barnacle (*Chthamalus*). Connell showed that at low intertidal levels where predators were abundant, the intensity of interspecific competition for space that *Chthamalus* suffered from *Balanus* was reduced by predators. Connell then concluded that the intensity of interspecific competition was less in the presence than absence of predators, and later generalized these results to other systems (Connell 1971, 1975). However, Connell's experiment did not explore the reciprocal effect of the

interaction between competition and predation on the superior barnacle species (*Balanus*). If this system conforms to the common observations that superior resource competitors are often more vulnerable to predators, we would expect that the effect of *Chthamalus* on *Balanus* would have been increased in the presence of predators.

Suggestions for future empirical and theoretical work, and their synthesis

Much remains to be learned about the interaction between predation and interspecific competition, both theoretically and empirically. What we already know suggests that the qualitative effect of predators on competition between prey species depends both on the aspect of competition that is being measured and on the details of the processes of competition and predation. We have therefore stressed the need to learn more about these processes, so that we may begin to accumulate data on the relative frequencies of different effects and different mechanisms. This will, of course, be a long, slow process. At the same time, the body of theory on the interaction of predation and competition is clearly incomplete. In this section we identify some areas where more theory is required, identify some important unanswered questions, and suggest strategies for achieving a closer connection between theory and empirical work.

Most of the theoretical work reviewed is based upon models with the following characteristics: populations are homogeneous in space; adaptive change, whether evolutionary or behavioural, is absent; there is no omnivory; species occur in food webs with at most three trophic levels; there are no time-lags between resource consumption and reproduction; and there are no within-species differences in terms of age, stage or physiological state. Each one of these is a major simplification, and each is likely to be violated in the vast majority of natural systems. In the case of every one of these simplifications, theorists have begun to explore models of competition, and in some cases the interaction between competition and predation, that incorporate more realistic assumptions (e.g. Slatkin 1974; Caswell 1978; Durrett & Levin 1994; Chase 1999; Connolly & Roughgarden 1999; Claessen *et al.* 2000; Diehl & Feissel 2000; Mylius *et al.* 2001; Shurin & Allen 2001). Such analyses are essential for revealing the extent to which conclusions derived from very simple models are likely to apply to natural systems, and for uncovering a variety of new mechanisms by which predation and competition interact.

A major area in which theory is lacking is the evolutionary consequences of predators for competition between prey species. Aside from one analysis of different mortality levels on the magnitude of character displacement in two-consumer-two-resource models (Abrams 1986), there does not appear to have been any thorough analysis of this

subject. However, future theory should not concentrate solely on more detailed models. New discoveries continue to be made about the behaviours of some of the simplest and best-established theoretical models for the population dynamics of competitors (e.g. Chesson 1990, 2000; Vandermeer 1993; Abrams 1998; Huisman & Weissing 1999, 2001). The importance of recycling of nutrients for the interaction of predation and competition is only beginning to be understood (DeAngelis 1992; Grover 1997, 2002; Grover & Holt 1998). Similarly, the population dynamical consequences of simultaneous predatory and competitive interactions between intraguild predators and their competitors or prey have only been touched upon (Holt & Polis 1997; Diehl & Feissel 2000; Mylius *et al.* 2001). Finally, a recent theoretical analysis by Shurin & Allen (2001) shows how predators can have different effects on prey species coexistence at local vs. regional spatial scales. Increasing study of metacommunity models should provide important insights here.

On the empirical side, knowing more about the relative frequencies of positive and negative effects of predation on coexistence would aid significantly in predicting some of the consequences of actual or potential human-caused environmental modification. Additions and removals of predators constitute one of the largest classes of human-induced environmental change. It would therefore be very useful to know more about the probable effects of such modifications on prey species diversity. This will require more empirical work. As we have emphasized, previous work has often not provided sufficient insight into interaction mechanisms to allow extrapolation to as yet unstudied systems.

We have also emphasized the importance of knowing the ratio of *per capita* inter- to intraspecific effects in understanding the interaction of predation and competition. In some systems, this ratio may be difficult to estimate. Nevertheless, it normally only requires that both inter- and intraspecific manipulations be performed, and there have been several studies that have estimated this ratio using a variety of methods (Spiller 1986; Abrams 1987; Pfister 1995; Chase 1996).

Most theory has concentrated on equilibrium conditions in closed systems. Most empirical attempts to estimate species interactions with and without competitors and predators were focused on transient, non-equilibrium dynamics and are typically performed in open systems. Theory needs to be able to predict outcomes expected from short experiments on small spatial scales in open systems. Further, both theory and manipulative experiments have concentrated on populations in homogeneous environments. We have emphasized the need for more theory regarding spatial and other forms of heterogeneity. This need also applies to experimental work, which has concen-

trated on manipulations over small spatial scales and uniform dispersion of resources (but see Petren & Case 1998; Chase *et al.* 2001).

There is considerable scope for increasing our knowledge of the effects of predators by measuring the effects of a wider range of predation rates, by measuring intraspecific as well as interspecific competitive effects, and by manipulating both members of a pair of competing species. None of these require radically new ecological methods. Thus, it seems likely that greatly increased insight into the mechanisms producing different interactions between predation and competition could be achieved relatively quickly. We foresee a future in which more detailed and diverse experiments combine with a more diverse and realistic set of models to provide a more comprehensive basis for predicting the consequences of altered predation on the coexistence of prey species.

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