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## POSITIVE INDIRECT EFFECTS BETWEEN PREY SPECIES THAT SHARE PREDATORS<sup>1</sup>

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**Abstract.** Mathematical models are used to explore the interaction between two prey species that share a common predator. The models assume that the predator experiences density dependence via some mechanism other than prey depletion. The models also assume that the predator's functional response to each prey decreases as the density of the other prey species increases. This can occur either because of predator satiation or predator switching. The results suggest that positive indirect effects of one prey on the equilibrium density of others should occur frequently, especially when there is predator switching. Decreasing the mortality rate of one prey or adding a prey species may make it easier for additional prey species to invade the system and coexist. This occurs because the resulting decrease in the predator's functional response is greater than its positive numerical response. In many cases, different magnitudes of perturbation to one prey species will have opposite effects on the population density of the other prey species.

**Key words:** *apparent competition; apparent mutualism; coexistence; density dependence; functional response; indirect effect; numerical response; predation.*

### INTRODUCTION

The indirect interaction between two prey that share a predator often represents the sum of effects transmitted by the predator's numerical and functional responses. Increases in the numbers of one prey often decrease the predator's functional response to other prey, either due to satiation or switching (Murdoch 1969, Murdoch and Oaten 1975); this tends to increase the numbers of the other prey. Alternatively or additionally, increases in the density of one prey increase predator numbers (a numerical response), which tends to reduce the numbers of the second prey species (Holt 1977, Holt and Lawton 1994). This potential conflict between the indirect effects due to functional and numerical responses has been noted by Holt (1977, 1984, 1987, Holt and Kotler 1987), Noy-Meir (1981), and Abrams (1983, 1987a, b, 1990a), among others. However, the balance between the two opposing indirect effects has not been explored quantitatively. This article analyzes some simple models to determine when mutually beneficial effects between prey are likely to occur via their shared predators.

As Holt (1977) has noted, there will always be mutually negative effects between prey via their shared predator if the predator's per capita growth rate is independent of predator density, given that all three species reach stable equilibrium densities. Under these

conditions the numerical response will always outweigh the opposing functional response. However, this need not be true when the predator's per capita growth rate decreases with predator density for reasons other than prey depletion (Holt 1977, Noy-Meir 1981, Abrams 1987a). All of the models we consider have such predator density dependence.

### DEFINITIONS AND METHODS

We will measure interactions by the change in the equilibrium density of one prey species caused by a change in the per capita death (harvest) rate of another prey species. Measuring indirect effects this way facilitates experimental studies because harvest rates may be changed in a continuous manner in most systems. If increasing the per capita death rate of one prey species increases the density of the other prey species, the interaction is negative (apparent competition if this is true for both species). If increasing the per capita death rate of the first prey species decreases the density of the other prey, then the first prey has a positive effect on the second; when this is true for both members of the pair, the interaction is apparent mutualism. Removal of one prey species corresponds to an increase in its per capita death rate large enough to cause extinction.

An increase in the density of one prey reduces the functional response to the other prey under (at least) two circumstances: (1) the predator reduces its general intensity of foraging when total prey density increases (saturation or satiation); or (2) the predator cannot hunt equally effectively for all prey simultaneously, and de-

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votes more attention to a given prey type, the more abundant it becomes (switching). Saturation can arise because of constraints on the predator's food processing capacity or because of adaptive reduction in the amount of costly foraging activities with increasing prey density (Abrams 1990b). Switching can arise because of adaptive habitat choice by the predator or because of adaptive search strategies within habitats (Murdoch and Oaten 1975, Abrams 1987b).

Our models assume that there is density dependence in the predator growth rate. Mechanisms for such density effects include: (1) predators compete for other resources required for population growth, such as shelter, nesting sites, water, etc.; (2) predators have their own parasites, diseases, and predators, which may increase in numbers or activity with increased predator density; (3) predator social behaviors such as aggression or grouping patterns may change with increased density in ways that reduce fitness; (4) antipredator behavior by the prey generally increases with predator density. Given that most predators in a food web are not top predators (Cohen et al. 1990), it is likely that a subset of point (2) is sufficient to lead to density dependence in most predator populations.

#### MODELS

The analyses address two questions: (1) If there is a single resident prey and a predator, how does the predation pressure on an invading prey species change as the per capita death rate of the resident prey is increased? (2) When two or more prey species are present at equilibrium with a common predator, how does an increased death rate of one prey affect the density of the other? In all of the analyses, parameters are chosen so that the equilibrium point is stable. When the equilibrium is unstable, the average density may change in a manner very different from the equilibrium density as harvest rates are changed (Abrams and Roth 1994). After deriving some general results, we illustrate them using two specific examples. Two types of predator density dependence affecting the predator's per capita death rate or its functional response are considered.

##### *Density dependence in the predator's death rate*

If  $N_1$  and  $N_2$  are the population densities of the two prey and  $P$  is the density of the predator, this situation can be modeled by

$$dN_1/dt = N_1 f_1(N_1) - C_1 g_1(N_1, N_2) P N_1 - d_1 N_1 \quad (1a)$$

$$dN_2/dt = N_2 f_2(N_2) - C_2 g_2(N_1, N_2) P N_2 - d_2 N_2 \quad (1b)$$

$$\begin{aligned} dP/dt = P \{ & b[E_1 C_1 N_1 g_1(N_1, N_2) \\ & + E_2 C_2 N_2 g_2(N_1, N_2)] \\ & - d_3 - a(P) \}, \end{aligned} \quad (1c)$$

where  $f_i$  is the per capita growth rate of prey species  $i$  in the absence of predation, and is a decreasing function

of  $N_i$ . The functions  $g_i$  describe the modification of the predator's maximum capture rate constant ( $C_i$  for prey  $i$ ) produced by saturation and/or switching;  $g_i$  has a maximum of 1. In the case of saturation,  $g_1 = g_2 = g$ , and  $g$  decreases with an increase in either population density. In the case of switching, by definition  $\partial/\partial N_1 [g_1/g_2] > 0$  and  $\partial/\partial N_2 [g_1/g_2] < 0$ . The  $E_i$  are relative caloric values of the two prey types. The function  $b$  describes the predator's assimilation and conversion efficiency of consumed food. The coefficients  $d_i$  are density-independent per capita death rates of predator ( $i = 3$ ) and prey ( $i = 1, 2$ ). The function  $a(P)$  describes the increase of the predator's per capita death rate with predator density. It is reasonable to assume that the predator does not reduce its caloric intake rate as the result of accepting either of prey species (Holt 1983). This means that  $\partial/\partial N_i \{E_1 C_1 N_1 g_1(N_1, N_2) + E_2 C_2 N_2 g_2(N_1, N_2)\} > 0$  for  $i = 1, 2$ .

Species 1 has a positive effect on species 2 if increasing the per capita death rate of species 1 by some amount  $\Delta d_1$  decreases the population density of prey species 2. For small values of  $\Delta d_1$ , a linear analysis generally yields a good approximation for the effect of the changed mortality on equilibrium population densities. We discuss the situation in which  $g$  reflects saturation rather than switching, because the analysis is simpler in this case. Theory developed by Bender et al. (1984) for the effects of press perturbations yields the following formula:

$$\partial N_2 / \partial d_1 = \{(-C_2)[gb'E_1 C_1(g + N_2 \partial g / \partial N_1) + Pa' \partial g / \partial N_1] / \text{Det}[M]\}, \quad (2)$$

where primes (') denote derivatives of functions with respect to their arguments, and  $\text{Det}[M]$  is the determinant of the Jacobian matrix whose elements are the partial derivatives of the three per capita growth rates in Eq. 1a–c with respect to the three population densities. Eq. 2 is obtained by setting the right-hand sides of Eq. 1a–c equal to zero, differentiating with respect to  $d_1$ , and solving the resulting set of linear equations for  $\{\partial N_1 / \partial d_1, \partial N_2 / \partial d_1, \partial P / \partial d_1\}$ . The stability of the equilibrium of the dynamic system (Eq. 1) implies that  $\text{Det}[M]$  must be negative. The sign of Eq. 2 is therefore determined by the relative magnitudes of two terms:  $gb'E_1 C_1(g + N_2 \partial g / \partial N_1)$ , which is always positive, and  $Pa' \partial g / \partial N_1$ , which is always negative. If the functional response is close to its asymptotic value, the first term approaches zero [ $(g + N_2 \partial g / \partial N_1) \approx 0$ ], and even the slightest amount of density dependence (small  $a'$ ) results in mutualism. Mutualism will also occur far from the asymptote of the functional response when the slope of the density-dependence function,  $a$ , is sufficiently large (given  $\partial g / \partial N_i \neq 0$ ). Even when Eq. 2 predicts a decrease in species 2 following small increases in  $d_1$ , a sufficiently large increase in  $d_1$  may increase species 2 (see example 1 below).

The indirect effect between prey may also be measured by the effect of the per capita death rate of one

prey species on the ability of a second prey species to invade the system. This is measured by the effect of  $d_1$  on the predation rate experienced by the second species when it is rare. Mutualism occurs when  $\Delta[Pg_2(N_1, 0)]/\Delta d_1 < 0$ , where population densities are at the single prey-predator equilibrium. An analytical formula can be obtained when  $g$  reflects satiation and  $\Delta d_1$  is small. The same methods used to derive Eq. 2 show that  $\partial(Pg(N_1, 0))/\partial d_1$  must have the same sign as  $\{a'(\partial g/\partial N_1) + gb'E_1C_1[N_1(\partial g/\partial N_1) + g]\}$ . This formula appears to be proportional to the numerator of Eq. 2, but it may have a different sign because the functions are being evaluated at different population densities ( $N_2 \approx 0$ ). Specifically, it is more likely to indicate a negative effect than is Eq. 2, because the satiation function  $g$  is further from its asymptote when only a single prey species is present. Nevertheless, the basic features are similar; the larger the slope of the predator density dependence or the closer the functional response is to saturation, the more likely it is that the effect of species 1 on 2 is positive. However, a very large increase in  $d_1$  will always eliminate the predator and make it easier for species 2 to invade.

Switching often results in positive effects under a wider range of conditions than does satiation because it may involve larger changes in the functional responses. However, it may be analyzed in a similar way and a larger slope of the density dependence function,  $da/dP$ , is again more likely to result in positive effects. As in the case of satiation, the sign of the effect often depends on the magnitude of the change in harvest rate.

In the remainder of this section, two examples are presented that illustrate the preceding general theory.

#### Example 1: predator satiation

Assume  $a$  and  $b$  in Eq. 1a–c are linear  $\{a(P) = AP$ , where  $A$  is a constant, and  $b = B[\Sigma C_i N_i g(N_1, \dots)]$ , where  $B$  is a constant}. Also, assume that the predator's functional response has the form of Holling's (1959) disk equation so  $g(N_1, N_2) = 1/(1 + C_1 N_1 H_1 + C_2 N_2 H_2)$ , where  $H_i$  is the handling time required for an individual of prey species  $i$ . Finally, assume that the prey species has logistic population growth; in the absence of predation,  $dN_i/dt = N_i(r_i - k_i N_i)$ . Bazykin (1974) has shown that there can be alternative stable equilibria for a range of parameter values in the single-prey version of this model. Whether or not there are alternative equilibria, decreasing the prey's per capita death rate when it is initially high is likely to first increase and then decrease the predation pressure on an invading prey species. This is illustrated in Fig. 1. When there are alternative equilibria, the effect of a given change in the prey's death rate on the predation rate has opposite signs at the two equilibria. At the equilibrium with a lower prey density, increasing the per capita death rate decreases predation pressure. Here effects are dominated by the predator's numerical response. At the equilibrium with the higher prey density, the functional

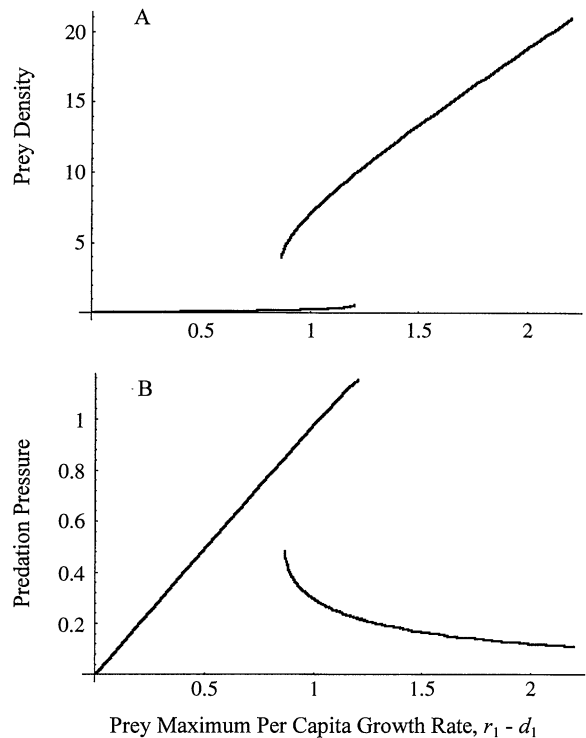


FIG. 1. The effect of the maximum (density independent) per capita growth rate of prey species 1 on its equilibrium density (A) and on the predation pressure (B) experienced by a rare second prey species (example 1). Increasing the per capita death rate reduces the maximum per capita growth rate. The parameters are:  $k = 0.1$ ;  $B = 5$ ;  $H_1 = 2$ ;  $C = 1$ ;  $A = 0.5$ ;  $d_3 = 0.1$ . There are two equilibrium points for growth rates ( $r_1 - d_1$ ) from 0.871 to 1.208. Predation pressure on an invader responds in opposite directions to a change in per capita growth rate at the two different equilibria.

response dominates, and increasing  $d_1$  promotes invasion.

The preceding analysis may also be applied to this example to examine indirect effects when both prey are present at equilibrium. At relatively high prey densities, the effect on the functional response predominates, while at low densities, the effect on the predator's numerical response is larger. Frequently, increasing the harvest of one prey from a low rate will initially decrease the density of the other prey. However, further increases in harvest will eventually increase the other prey's density, as the effect on the numerical response begins to overcome the effect on the functional response. Fig. 2 illustrates the effect of one prey's per capita death rate on the equilibrium density of the other prey. We have chosen parameter values for which there is only a single stable equilibrium point for all prey death rates. First consider the sign of the interaction when both prey have the same maximum per capita growth rate;  $r_1 - d_1 = r_2 - d_2 = 1$ . If  $A = 0.1$ , small decreases in the death rate of species 2 decrease the density of species 1, indicating a negative effect on

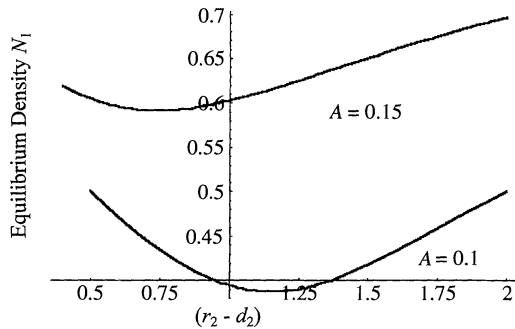


FIG. 2. The effect of the maximum density-independent per capita growth rate of prey species 2 on the equilibrium density of prey species 1, for two different values of the predator interference parameter,  $A$ . The model assumes logistic prey growth, a disk equation predator functional response, linear predator density dependence, and a linear predator numerical response. The other parameter values are,  $C = 1$ ;  $B = 1$ ;  $H_1 = H_2 = 2$ ;  $k_1 = k_2 = 1$ ;  $E_1 = E_2 = 1$ ;  $d_3 = 0.15$ ;  $r_1 - d_1 = 1$ .

species 1. However, the opposite is true when  $A = 0.15$ . The sign characterizing this interaction can change with the magnitude of the change in  $d_2$ . Large decreases or large increases in the death rate of species 2 will each increase the population density of species 1 for both values of  $A$ . Greatly increased death rates have negative effects because lower total prey density makes the numerical response larger than the functional response. Similar effects would occur in systems with more than two prey species. As the number of noncompeting prey species increases, the predator functional response saturates, and each successive species added to the system is more likely to increase the densities of the resident species.

#### Example 2: adaptive switching

Switching often arises because two prey types cannot both be captured at maximum rates simultaneously. The predator experiences a trade-off between its two prey capture rates. This can be modeled by making  $g_2$  a decreasing function of  $g_1$ . The value of  $g_1$  is adjusted behaviorally to maximize the predator's fitness. We further assume that handling times are insignificant. Given linear forms for the functions  $f_i$ ,  $b$ , and  $a$ , we obtain the following conditions at equilibrium:

$$0 = r_1 - k_1 N_1 - C_1 g_1 P - d_1, \quad (3a)$$

$$0 = r_2 - k_2 N_2 - C_2 g_2(g_1)P - d_2, \quad (3b)$$

$$0 = B(E_1 C_1 g_1 N_1 + E_2 C_2 g_2 N_2) - D - AP, \quad (3c)$$

$$0 = C_1 E_1 N_1 + C_2 (dg_2/dg_1) E_2 N_2, \quad (3d)$$

where  $A$ ,  $B$ ,  $r_i$ , and  $k_i$  are constants. The fourth equation in this set is an equilibrium condition for a dynamic equation describing the change in trait values. We assume here that trait dynamics are much more rapid than population dynamics, and that they result in consump-

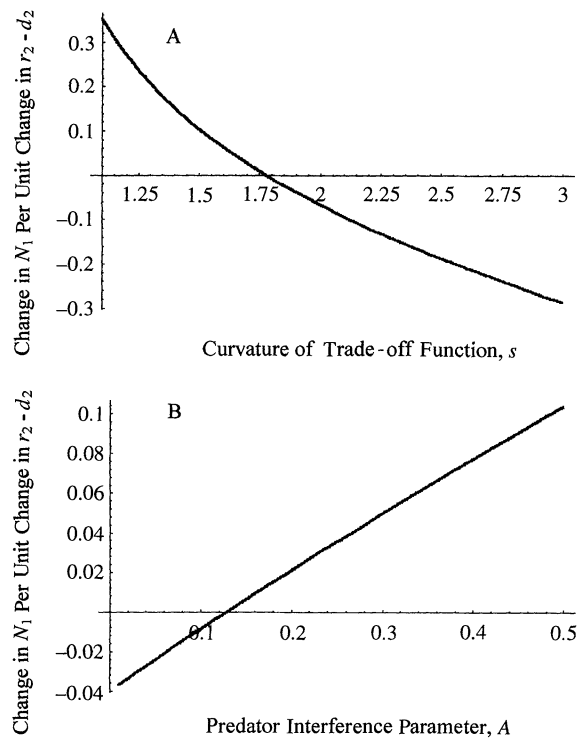


FIG. 3. The effect of a change in the per capita growth rate of species 2 on the equilibrium density of species 1 for a model with a switching predator functional response. The growth functions of the two prey species are initially identical with  $r_i - d_i = 1$ , and  $k_i = 0.1$ . Positive values indicate mutualistic interactions, while negative values indicate apparent competition. Fig. 3A, B illustrates the effects of  $s$  and  $A$ , respectively. Larger values of  $s$  reflect a greater curvature in the trade-off relationship between  $g_1$  and  $g_2$ . Larger values of  $A$  reflect greater predator density dependence. Parameter values are  $B = 1$ ;  $d_3 = 0.2$ ;  $E_1 = E_2 = 1$ . In Fig. 3A,  $A = 0.5$ ; in Fig. 3B,  $s = 1.5$ .

tion rates that maximize individual fitness ( $d^2 g_2 / dg_1^2 < 0$ ). For simplicity, we assume that  $C_1 = C_2 = 1$ . A relatively flexible form for the trade-off relationship between  $g_1$  and  $g_2$  is:

$$g_1^s + g_2^s = 1, \quad (4)$$

where the exponent  $s$  is  $>1$ , and larger values of  $s$  imply that it is possible for the predator to achieve close to its maximum consumption rate of both prey simultaneously. Fig. 3 shows that small values of the trade-off curvature parameter,  $s$ , or large values of the predator interference parameter,  $A$ , both tend to make the interaction between prey mutualistic. When the trade-off is close to linear, the interaction of the two prey species is mutualistic for a wide range of death rates, because this results in maximal switching (see Holt 1987). However, strongly curved relationships ( $s \gg 1$ ) result in apparent competition, unless the predator's density dependence is particularly strong ( $A$  large). Fig. 3 is based on a system in which both prey have similar maximum



growth rates, and the death rate of one species is only changed by a small amount. As before, the direction of the change in  $N_i$  with a change in  $d_j$  can depend on the magnitude of the change in  $d_j$ , as in Fig. 2.

*Density dependence in the predator functional response*

The above analysis assumed that the predator experienced density dependence from resources or factors that operate independently of food intake rate. However, if searching predators engage in time-consuming behavioral interactions when they encounter each other, then their functional responses to all prey types will decline as predator density increases (DeAngelis et al. 1975). Another common reason for predator density dependence via functional responses is because of adaptive antipredator behavior by the prey (Abrams 1991). Increases in predator density provoke greater levels of antipredator behavior, reducing the predator's capture rate. The predator's functional response to the prey exhibiting antipredator behavior then declines with increasing predator density. However, the antipredator behavior of a given prey species need not reduce the predator's response to other prey species. Here we will consider predator density dependence resulting from both of these factors.

If the predator's density dependence results from aggressive behavior while foraging, Eq. 1a–c can be modified by making the saturation/switching functions,  $g$ , decrease with  $P$ , and by removing the other density-dependent function,  $a$ , from Eq. 1c. We will only present an analysis of invasion by a second prey species under these conditions, given a saturating functional response. The effect of changing the resident's death rate  $d_1$  on predation pressure,  $Pg$ , is

$$\frac{\partial}{\partial d_1}(Pg) = \frac{g[P(\partial g/\partial P) + g + N(\partial g/\partial N)]}{\left\{ N\left(\frac{\partial g}{\partial P}\right)\left[b + CP\left(\frac{\partial g}{\partial N}\right)\right] - C\left[g + P\left(\frac{\partial g}{\partial P}\right)\right]\left[g + N\left(\frac{\partial g}{\partial N}\right)\right] \right\}} \quad (5)$$

where all derivatives and population densities are evaluated at the equilibrium point. Like Eq. 2, this formula is a straightforward application of the formulas developed by Bender et al. (1984) for responses to press perturbations. The denominator of the expression must be negative if the equilibrium point of the dynamic system is to be stable. Because  $\partial g/\partial P$  is negative, a sufficiently large amount of interference between predators can, in theory, make the numerator of Eq. 5 negative, generating a positive effect of the resident on an invading prey species. However, there are limits on the magnitude of the interference term  $\partial g/\partial P$ . As prey become abundant and the predator's functional response saturates,  $g$  becomes small, and the derivative  $\partial g/\partial P$  must also become small. This means that conditions

for positive indirect effects between prey may be restrictive (or, for some types of interference, nonexistent). As an illustration, consider the following functional response, proposed by DeAngelis et al. (1975):

$$g = C_1 N_1 / (1 + C_1 H_1 N_1 + AP), \quad (6)$$

where  $A$  is a constant representing the amount of search time lost with each encounter with another predator. Eq. 5 is always negative, given this functional response, meaning that indirect effects between prey are negative. This conclusion remains true if  $AP$  is replaced by any positive relationship  $a(P)$  between predator density and lost search time. Thus, predator interference via the functional response is unlikely to reverse "apparent competition" between shared prey when the functional response only involves saturation. However mutualism is more likely when there is a switching response.

## DISCUSSION

The analysis presented here predicts that prey sharing common predators should often have positive effects on each other's density. Such effects seem most likely when: (1) the predator exhibits switching or a strongly saturating functional response; (2) the predator's per capita death rate increases rapidly with predator density; and (3) the change in the predator's death rate used to measure the effect is relatively small. The biological conditions, saturating or switching functional responses and some density dependence in predator death rates, are likely to be common occurrences. However, we have not been able to find documented field examples of such positive long-term indirect effects between prey. This lack of data has two possible explanations: (1) the conditions required for the positive effects occur infrequently; (2) positive effects occur, but they have been undetected, ignored, or misinterpreted. We favor the second explanation.

An absence of predator density dependence would imply either a lack of significant higher level predators and parasites, or that the densities of such predators and parasites are independent of their food supply. This seems unlikely based on our present knowledge of food webs (Cohen et al. 1990) and parasites (e.g., Price 1980, Anderson 1989). Other factors such as aggressive behavior and limited supplies of high quality shelter, nesting sites, etc., provide additional reasons for believing that some non-food-related density dependence is the rule in consumer species. Hassell (1978) argues that the vast majority of predator functional responses saturate, and this is a logical necessity at sufficiently high prey densities. Switching predation has been documented in a smaller number of systems (e.g., review by Murdoch and Oaten 1975), but this scarcity of examples may result from the relative scarcity of functional response studies involving two or more prey (Abrams 1987b, 1990b). We are not aware of any studies of functional responses on two or more prey that searched for, but failed to find either one or both of these two types of

nonlinearity. If the above summary is an accurate representation of the prevalence of density dependence and nonlinearities in functional responses, positive effects would only be absent if these two factors are generally small in magnitude. This cannot be ruled out, but there are counterexamples that argue against small effects. Some functional response studies have found virtually no response across most of the natural range of prey densities (Messier 1994 for wolves, and Abrams et al. 1990 for an annelid worm). Such extreme levels of saturation should generate large positive effects between prey species. If most species do not experience density dependence except via food and predators, then theory (Oksanen et al. 1981) argues that species that are odd numbers of trophic levels from the top of the system will be limited by their own predators and have absolutely no numerical response at equilibrium. Pimm (1991), Oksanen et al. (1981), and Persson et al. (1992) review evidence for this idea.

It seems likely that positive indirect effects between shared prey have been overlooked. There are (at least) two possible reasons. First, most perturbation experiments have involved removal or addition of prey rather than small changes in harvesting rates (Holt and Lawton 1994), and the latter are more likely to produce positive effects. Secondly, observations that are inconsistent with prevailing theory are often overlooked. When Holt (1977) first publicized the idea of apparent competition, he found little evidence for the occurrence of negative indirect effects between prey. However, Holt and Lawton's (1994) recent review lists a substantial number of studies. One frequently cited demonstration of apparent competition is Schmitt's (1987) study of the interaction between bivalves and several herbivorous snail species as the result of shared predation by mobile predators. Bivalves and snails are generally found in different habitats (high-relief and cobble habitats, respectively). When bivalve densities were increased in the cobble habitat, predators (mainly octopus and lobster) moved into the area, causing a fourfold increase in mortality of the snails. Because this effect was based on predator movement, it seems likely that prey species in the high-relief habitat from which the predators moved experienced positive effects from the increase in bivalves in the cobble habitat. However, these effects were not reported or quantified. It is likely that they would have been studied in greater detail, had there been a more widely known body of theory predicting positive effects via shared predation.

Field experiments in multispecies communities involve many more indirect pathways than those between the focal species. Simply finding a positive effect of one prey species on another would not guarantee that the mechanism described here was responsible.

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