

APPARENT COMPETITION OR APPARENT MUTUALISM? SHARED PREDATION WHEN POPULATIONS CYCLE

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Abstract. We use simple mathematical models to explore the indirect interactions between two prey species that share a predator when all three species undergo population cycles. The results are compared to analogous findings for systems that reach a stable equilibrium point. It is common for removal of one prey from a cycling system to result in a decrease in the mean density of the remaining prey species, contrary to the usual logic of apparent competition. Even when apparent competition between prey exists, its magnitude is usually reduced by population cycles. This effect occurs when the predator has a concave-down relationship between prey abundance and its own per capita growth rate. Such relationships can occur because of a saturating functional or numerical response. We investigate how prey density dependence and the shape of the predator's functional and numerical responses affect the sign and magnitude of this indirect interaction between prey species. There may also be (+, -) interactions between prey that differ significantly in their susceptibility to the common predator.

Key words: *apparent competition; apparent mutualism; environmental variation; indirect effects; limit cycles; shared predation.*

INTRODUCTION

Few, if any natural populations are constantly at equilibrium densities. Variation in the weather and other environmental parameters results in what we will term exogenous variability in populations. Endogenous variation is generally driven by strong or time-lagged intraspecific density dependence or by interspecific interactions such as predation. Laboratory predator-prey systems are notorious for their tendency to cycle (Taylor 1984). Recent analysis of a variety of time series of population densities from natural populations (Turchin and Taylor 1992, Ellner and Turchin 1995) suggests that natural populations exhibit a full range of dynamic behaviors, from stable equilibria, through damped oscillations, to sustained cycles and chaos. Population densities in some species vary over 3–4 orders of magnitude or more (Williamson 1972).

The recognition that many populations undergo sustained variation has not been accompanied by a corresponding amount of attention to the broader implications of such dynamics. There has been some recognition that variation can be important in influencing interactions in nonlinear systems (Chesson 1978, 1986, 1991, Levins 1979, Armstrong and McGehee 1980, Abrams 1987*b*). More recently, Abrams and Roth (1994*a, b*; see also Abrams et al. 1997) have pointed out that cyclic or chaotic dynamics can change the qualitative nature of interactions between species in simple food chains. They show that an environmental

change that increases (decreases) the density of a species when it occupies a stable equilibrium may have the opposite effect on the time-averaged density when the species undergoes limit cycles or chaos.

The present article will analyze the effects of endogenous variation in a system with two (or more) prey species that share a common predator. Just as consumer species can reciprocally reduce each other's abundance via depleting a shared resource, prey species can sometimes indirectly depress each other by increasing the abundance of a shared natural enemy, an effect called apparent competition (Holt 1977, Holt and Lawton 1993). This phenomenon had received very little attention from ecologists before Holt's (1977) theoretical analysis. That and subsequent work stimulated a large number of field studies; Holt and Lawton (1994; 497) summarize the experimental and observational evidence, saying, "There are literally hundreds of examples we could use to illuminate how alternative prey for generalist predators influence the distribution and abundance of focal victim species." These studies range from protist assemblages in laboratory microcosms to interactions between sea urchins and the city of Los Angeles. For additional examples, see Holt and Lawton (1994) or reviews by Connell (1990) or Reader (1992), which consider interactions via shared herbivores.

Holt (1977) showed that apparent competition arose in systems with one predator feeding on multiple prey under three broad assumptions: (1) the predator was strictly food-limited (i.e., the per capita growth rate of

the predator can be expressed as a function of prey availability), (2) the predator had a positive numerical response to each prey, and (3) the system settled into a point equilibrium. It is known that relaxing either of the first two assumptions tends to weaken apparent competition (Holt 1977, 1987, 1996, Abrams and Matsuda 1996). In this paper, we concentrate on the third assumption, and examine the implications of sustained fluctuations in population densities on the indirect effects between shared prey. This is important because many of the well-known examples of cycles, such as the lynx-hare cycle, occur in systems that have two or more prey species (Royama 1992).

To compare our results with earlier ones based on stable systems, we remind readers of some of the major qualitative factors affecting the extent of apparent competition. Given the above three assumptions, prey with high values of the ratio of intrinsic growth rate to attack rate by predators can potentially exclude prey with lower values. The likelihood of exclusion depends upon the predator's capacity to limit prey numbers to levels at which they experience little density dependence; increases in prey carrying capacities therefore magnify the potential for exclusion of one or more prey species. Shared prey interact via the predator's functional response as well as its numerical response. If the functional response saturates at high densities, and if the predator's density is limited by factors other than its consumption of prey, then positive indirect interactions between prey may occur (Holt 1977, Noy Meir 1981, Abrams and Matsuda 1996).

WHEN AND WHY DOES CYCLING ALTER APPARENT COMPETITION?

As a prelude to the more specific models analyzed in detail below, the following argument provides a general framework for understanding when and why cycling of population densities may alter apparent competition. Table 1 defines all of the symbols used in equations. Consider a system where a predator persists with either of two alternative prey species. The dynamics of the predator (P) and a single resident prey (N_1) are described by

$$(1/N_1)dN_1/dt = f_1(N_1) - C_1g(N_1)P \quad (1a)$$

$$(1/P)dP/dt = b(C_1g(N_1)N_1) \quad (1b)$$

where f_1 is a decreasing function of N_1 , giving the per capita growth rate of prey species 1; C_1N_1 is the maximum prey capture rate by an average predator, g describes how this maximum capture rate decreases with prey density due to saturation of the predator's functional response (i.e., the functional response on prey 1 is $C_1g[N_1]$); and b is the predator's per capita growth rate as a function of its prey intake rate (i.e., b is the numerical response; b is an increasing function and $b = 0$ for some finite intake rate). Addition of a second prey that is nutritionally substitutable (Leon and Tump-

TABLE 1. Definitions of symbols and parameters.

| | |
|------------|---|
| N_i | population density of prey species i |
| P | population density of the predator |
| f_i | prey per capita growth rate function |
| g | predator satiation function |
| b | predator per capita growth rate function |
| C_i | per prey capture rate of prey by an unsatiated predator |
| e_i | nutritional value of prey i to the predator |
| r_i | intrinsic rate of increase of prey i |
| K_i | carrying capacity of prey i |
| θ_i | exponent describing the strength of density dependence in prey per capita growth rate |
| h_i | handling time required for the predator to consume an individual of prey i |
| d_i | per capita harvest rate of prey species i |
| T | energy or nutrient intake required for zero population growth of prey |
| α | scaled consumption rate parameter ($=KeC/r$) |
| β | scaled handling time parameter ($=KhC$) |
| D | scaled energy/nutrient requirement ($=T/r$) |
| B | the maximum per capita predator growth in the model with a hyperbolic numerical response |
| δ | parameter scaling the effect of food intake on predator growth in the model with a hyperbolic numerical response |
| γ | parameter in type-3 functional response models that determines the nonlinearity of the response at low prey densities |

son 1975) for the first prey, but does not compete with that prey for resources, leads to the following model:

$$(1/N_1)dN_1/dt = f_1(N_1) - C_1g(N_1, N_2)P \quad (2a)$$

$$(1/N_2)dN_2/dt = f_2(N_2) - C_2g(N_1, N_2)P \quad (2b)$$

$$(1/P)dP/dt = b(e_1g(N_1, N_2)C_1N_1 + e_2g(N_1, N_2)C_2N_2) \quad (2c)$$

where predator satiation, g , is now a function of the densities of both prey species, and the e_i are relative nutritional values of the two prey species. If the environment is variable, any or all of the functions and parameters in Eqs. 1 and 2 may also be explicit functions of time.

Understanding the effects of population cycles in the single-prey system is essential for understanding interactions in the two-prey system. If the solutions of Eqs. 1a and b exhibit sustained and bounded population fluctuations, the long-term time-average of each species' per capita growth rate must be zero (Levins 1979). Results discussed in Hofbauer and Sigmund (1988) show that, if the per capita rates of increase of all species are linear, time-independent functions of population densities (g constant; f and b linear in Eqs. 1), the asymptotic mean densities in cycling systems must equal the densities at an interior equilibrium point. However, this is no longer true in general when per capita growth rates are nonlinear. Upper limits on the predator's consumption rate of prey imply that the satiation function, g , decreases at large values of N_1 ($g' < 0$), and g often decreases over the entire range of

prey densities. Upper limits to reproductive capacity imply that the predator's numerical response function b will be concave at high prey densities ($b'' < 0$). The shapes of both functions (g and b) imply that increased variation in prey density must reduce the mean predator growth rate, compared to a constant environment with the same mean prey density. Chesson (1991) refers to this as a positive nonlinearity; the reduction in mean predator growth rate with increasing variation in prey numbers is a consequence of Jensen's Inequality. Over the long term, the time-average of the numerical response b must be zero. However, decreases in prey density produce a larger effect on predator growth than do increases of equal magnitude. Consequently, when prey variability increases, a larger average prey density is required to achieve zero population growth of the predator. For this reason, factors that increase the amplitude of population cycles increase mean prey density in Eqs. 1 (Armstrong and McGehee 1980, Abrams and Roth 1994a, Abrams et al. 1997).

The addition of a second, similar prey species ("similar" here means that f_1 and f_2 have the same functional form; $C_1 = C_2$; $e_1 = e_2$; g is a function of $N_1 + N_2$) to a one-predator one-prey system often has effects on system stability similar to doubling the carrying capacity of the original system. When the two prey have identical logistic growth functions, the condition for limit cycles in the two-prey system is identical to that in a one-prey system with a doubled carrying capacity (Abrams 1987a). When addition of a second prey is destabilizing, the increase in the mean density of the original prey due to the initiation of cycles, or to greater amplitude of cycles, may outweigh any decrease due to the possibly higher predator densities engendered by the second prey species. Increasing the carrying capacity of the prey in a one-prey one-predator system often decreases or has little effect on the average predator density (Abrams and Roth 1994a, Abrams et al. 1997). This is because the negative effect on the predator due to increased variability of the total prey population offsets the positive effect of a larger mean total prey density. Thus, changes in mean predator density following addition of a second prey species may be small or negative, and may fail to generate much "apparent competition" in cycling systems.

It is important to note that there must be some density dependence in the reproductive rates of two prey species if they are to coexist when they share a common, food-limited predator, even when there are sustained fluctuations in density (Holt 1996). This can be seen by considering the fate of an invasion by small numbers of a second prey species into a system consisting of one prey and one predator (Eqs. 1). Here and subsequently we use $\langle x \rangle$ to denote the long-term arithmetic time-average of the quantity x . When there is no density dependence ($df_i/dN_i = 0$ for all N_i), the mean predation pressure on the resident prey species, $\langle gC_1P \rangle$, must equal the mean density-independent reproductive rate

of prey 1, $\langle f_1 \rangle$. Assume that the second prey is attacked at a rate proportional to the resident, i.e., $C_2 = \mu C_1$. A second species can only invade if its mean reproductive rate, $\langle f_2 \rangle$ is greater than $\langle gC_2P \rangle = \mu \langle gC_1P \rangle = \mu \langle f_1 \rangle$. However, if this is true, the second species will exclude the first, because it will support an average predation pressure too great for prey 1 to increase when rare. Some density dependence in the prey is thus required for coexistence, even in the presence of population fluctuations. Variability can be thought of as promoting coexistence of shared prey by enhancing the effects of intraspecific direct density dependence, and by increasing the relative importance of effects transmitted via the predator's functional rather than its numerical response.

There has been a tendency for ecologists to believe that average densities in cycling systems respond to environmental parameters in the same direction as does the equilibrium point associated with the cycle. Because limit cycles associated with an equilibrium point surround that point in state space in two-dimensional systems, this idea might initially appear plausible. However, drastic changes in the shape and amplitude of cycles may accompany changes in stability-determining parameters. As a result, equilibrium densities and average densities in unstable nonlinear systems often change in opposite directions in response to an environmental perturbation.

Before analyzing specific models, we must discuss the definition of interspecific effects in the context of cycling populations. Above, we have implicitly measured effects based on changes in the arithmetic mean density of the focal species over time. This has been the most common method of summarizing population densities in models with temporal variability (e.g., May 1973), as well as in statistical summaries of field data. Arithmetic mean densities are often the most informative single statistic for invasion analyses. For example, if a prey species with maximum per capita growth rate r is to be able to increase from low densities, r must be greater than the predator attack rate multiplied by the temporal arithmetic mean of predator density. However, when densities fluctuate, the effect of one species on another cannot be completely described by its effect on mean density. Some statistics, such as minimum density, may respond to an environmental change in a direction opposite to the arithmetic mean. If one is interested in inbreeding effects, the harmonic mean density of a species may be of more interest than the arithmetic mean. In the following analysis, we concentrate on the arithmetic mean, but also include some consideration of other population statistics.

MODELS AND ANALYSIS

General framework

The preceding argument cannot tell us much about the magnitude of the impact of population cycling on

indirect effects via a shared predator. Simulation of specific models is required. An infinite array of models fit the framework of Eqs. 2, and it is clearly impossible to investigate all variations. Our approach here is to concentrate on models that have frequently been used in previous analyses of predator-prey systems. We begin by analyzing the most commonly discussed model in the predator-prey literature that may exhibit limit cycle behavior. We then examine the consequences of altering the model in ways that seemed likely to change apparent competition, based on previous work on single prey-predator systems. Models in which the two prey have similar dynamics (i.e., symmetrical systems) are explored in some detail, because the mechanism producing effects on mean densities is particularly clear in this case. More limited results for systems that are not symmetrical are also presented.

We will define and measure indirect effects in two different ways. We first consider the change in the mean density of one (of two) prey species following the removal of the second species. In cycling systems, this is an average over the course of a cycle, after the system has converged to its long-term dynamic behavior. For some of the models, we also consider the change in mean density of one prey produced by a change in the density-independent per capita death rate of the focal species (Bender et al. 1984, Abrams and Matsuda 1996). This can be done straightforwardly by subtracting an additional per capita death (harvest) rate, denoted d_i , from the per capita rate of increase of prey species i given by Eq. 2a or 2b. The theory developed for stable systems suggests that removing one prey will increase the density of the other, and increasing the per capita harvest rate of one species will increase the density of the other.

In all cases, numerical integrations were carried out using two different integration procedures to check for the possibility of numerical errors (fourth-order Runge-Kutta with adaptive variation in step size, as implemented in Mathematica [version 2.2.3, Wolfram 1994] using the command NDSolve with a setting, "AccuracyGoal→Infinity"; and the Burlish-Stoer method [coded in FORTRAN following Press et al. 1986]). The dynamics were judged to have converged to the limit cycle when the mean densities of each of the three species had not changed by >0.001% over the course of five previous cycles. Average densities were calculated using Mathematica.

The basic model

We begin by considering one-predator two-prey versions of what is probably the most common predator-prey model in the ecological literature (e.g., see Yodzis and Innis 1992 and references therein). This is characterized by a logistic or modified logistic prey growth function, a linear predator numerical response (b), and predator functional responses, $C_i N_i g_i$, given by the mul-

ti-species version of Holling's (1959) disk equation. Thus,

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \left(\frac{N_1}{K_1} \right)^{\theta_1} \right) - \frac{C_1 N_1 P}{1 + h_1 C_1 N_1 + h_2 C_2 N_2} - d_1 N_1 \quad (3a)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \left(\frac{N_2}{K_2} \right)^{\theta_2} \right) - \frac{C_2 N_2 P}{1 + h_1 C_1 N_1 + h_2 C_2 N_2} - d_2 N_2 \quad (3b)$$

$$\frac{dP}{dt} = P \left(\frac{e_1 C_1 N_1 + e_2 C_2 N_2}{1 + h_1 C_1 N_1 + h_2 C_2 N_2} - T \right) \quad (3c)$$

where r_i is the intrinsic growth rate and K_i is the carrying capacity of prey species i , C_i is the per-prey capture rate of prey i by a searching predator, and e_i and h_i are the energy (or nutrient) content and handling time for that prey. The parameter T represents the energy (or nutrient) intake rate required for zero population growth of the predator, and θ_i is a parameter describing the form of density-dependent growth in prey species i (see Gilpin and Ayala 1973 or below for a discussion of this "theta-logistic" model of growth). Harvesting is represented by the $d_i N_i$ terms in each prey equation; these terms are included so we can measure the indirect effects from small changes in harvest rates. The stability of this system is discussed in Abrams (1987a); sufficiently high capture rates or a low predator energy requirement will lead to limit cycles, and, for reasons sketched below, the two-prey system is more likely to be unstable than is the system with a single prey species.

Several of the 11 parameters in Eqs. 3 can be removed by scaling, but the parameter space is still too large for a systematic investigation. The results we present here are therefore a sample of phenomena that occur in this system rather than a complete catalogue. We concentrate on symmetrical systems in which the two prey have identical population growth parameters. This enables the number of parameters to be reduced to four (three, if we also assume $\theta_i = 1$), and the parameter space can be explored in a relatively complete manner. In this initial analysis of Eqs. 3 we only compare the mean prey densities in corresponding systems with one or both prey species present (and both $d_i = 0$). In a later section we examine the effects on mean densities of a continuous range of harvest rates for one species, with the second species having a fixed harvesting rate; such harvesting makes the systems asymmetrical.

The basic symmetrical system

Assuming equivalent logistic growth functions of the two prey ($\theta = 1$), rescaling the variables and assuming the $d_i = 0$ allows Eqs. 3 to be rewritten as

$$dN_i/dt = N_i(1 - N_i) - \alpha N_i P / (1 + \beta N_1 + \beta N_2),$$

$$i = 1, 2 \tag{4a}$$

$$dP/dt = P[(\alpha N_1 + \alpha N_2) / (1 + \beta N_1 + \beta N_2)] - D \tag{4b}$$

where time is rescaled to the intrinsic growth rate, N is rescaled as N/K , P is rescaled as P/Ke , and $\alpha = KeC/r$, and $\beta = KhC$, and $D = T/r$. We initially examined indirect effects defined by the change in mean density of one prey species caused by removal of the other prey species. This was done for parameters that spanned the range producing biologically reasonable cycles in either one- or two-prey systems. Any set of parameter values producing a range of density of 10 or more orders of magnitude was considered to be unrealistic; this requirement sets a lower limit on D and an upper limit on α (Gilpin 1975, Yodzis and Innis 1992). Values of β larger than 10 were not considered because these imply that >95% of the predator's time is occupied with handling prey when prey are at their carrying capacities. The β values examined were {0.75, 1.5, 3, 6, 10}; these span the range of those large enough to produce cycles, but not so large as to give unrealistic total handling times. For each value of β we simulated systems with per capita capture rate equal to, significantly smaller than, and significantly larger than the prey's maximum growth rate ($\alpha = 1$, $\alpha = 0.2$, $\alpha = 5$). For each combination of α and β , we examined the full range of permissible D values that produced cycles in two-species systems that were not of excessive magnitude. Fig. 1 shows the relative change in the mean density of one prey species when the second, equivalent prey species is removed for all of these combinations. Each of the three parts of the figure assumes a different value of α ; each line assumes a different value of β , and shows the effect of removing one species for a range of predator intake requirements (D values.). The largest D value examined in each case is the smallest value for which the two-species system is stable. Our rejection of cycles greater than 10 orders of magnitude may be too lenient; if cycles were required to be of <5 orders of magnitude, the minimum D values would be slightly higher, but none of the following conclusions would be changed significantly.

When this system has a stable equilibrium, (e.g., when D is sufficiently large), there is always a 100% increase in the remaining species when the second prey species was removed. It is clear from Fig. 1 that the presence of cycles reduces the extent of apparent competition for all parameter values. For some parameter values, the indirect interaction between prey is mutualistic (i.e., there was a negative change in mean density following removal of the other prey), although the mutualistic effects are smaller than the competitive effect that occurs in stable systems. Mutualism is unlikely when the handling time, reflected in the parameter β ,

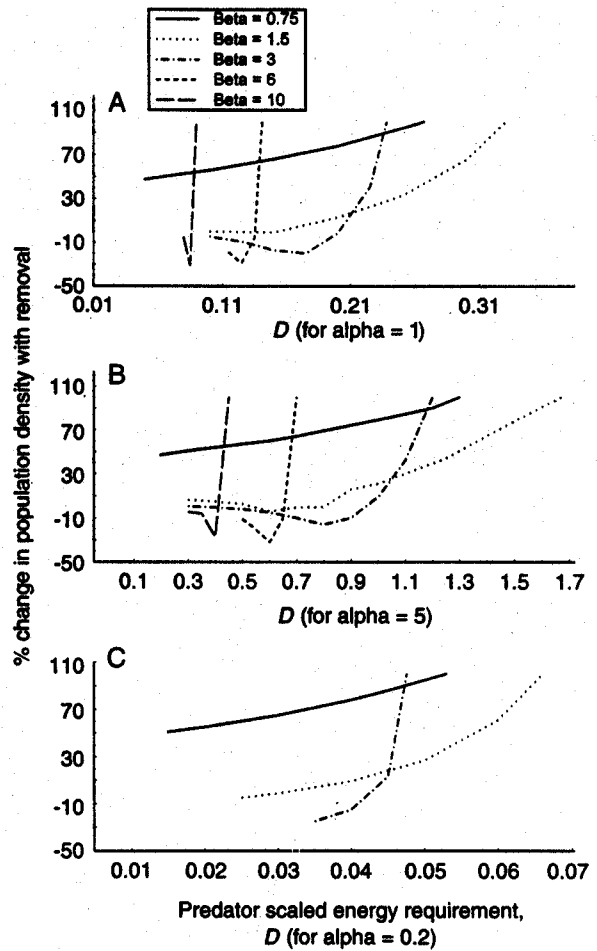


FIG. 1. Percentage changes in population density following removal of a second, equivalent prey population, based on simulations of Eqs. 4. Positive values indicate apparent competition, while negative values indicate mutualism. A, B, and C illustrate systems with different values of the scaled capture rate parameter α ; lines represent different values of the scaled predator death rate parameter D for several different values of the scaled handling-time parameter β .

is either very small or very large. When β is large (e.g., $\beta = 6$ or $\beta = 10$ in Fig. 1A and B), only a narrow range of D values result in biologically plausible cycles. When β is small (0.75), the nonlinearity of the functional response is not sufficient to generate mutualism. Fig. 1C also shows that a low predator conversion efficiency (e in Eqs. 3 or α in Eqs. 4) makes mutualism relatively unlikely. However, there exist a broad range of intermediate handling times and predator energy requirements that result in mutualism in Fig. 1A and B. When mutualistic interactions occur, it is either for predator energy requirements, D , below a threshold, or for a range of intermediate values of D within the larger range that produces reasonably behaved cycles. When D is just below the maximum value producing cycles in the two-prey system, the cycles are

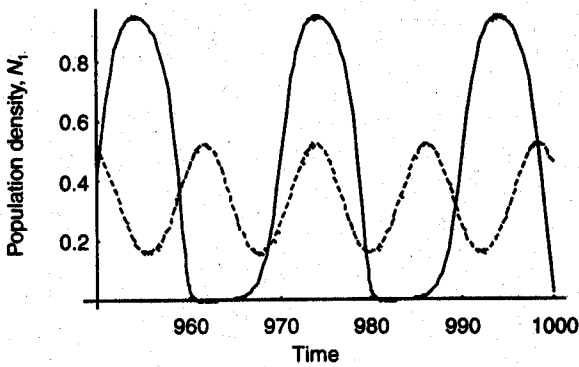


FIG. 2. Population density of prey species 1 in a single-prey system (dotted line) and a two-prey system with equivalent prey species (solid line), undergoing limit cycle oscillations based on Eqs. 4. The parameters are $\alpha = 5$, $\beta = 3$, and $D = 0.8$.

not sufficiently extreme in period and amplitude to greatly change the mean population densities from the equilibrium values, and there is a high level of apparent competition. When D is very small, cycles are of extreme amplitude in both one- and two-prey systems. Thus, the greatest mutualism is often observed when D has an intermediate value; the addition of a second species then most strongly magnifies the consequences of the nonlinearity in predator response.

Fig. 2 illustrates the consequences of decreased stability following addition of a second prey species; the amplitude and period of oscillations in the resident prey are greater when a second prey species is added (solid line) than when the resident prey alone is present (dashed line). Although the minimum density in the two-prey system appears to be close to zero, it is actually ~ 0.001 times the maximum density. Cycles in natural systems frequently have a greater amplitude than this (Royama 1992). The addition of the second

prey results in a 16% increase in the mean density of the resident prey in the case illustrated in Fig. 2.

Thus far, we have only considered systems in which prey growth is logistic ($\theta = 1$). If the prey have non-linear density dependence, the nature of their indirect interaction may change. The larger the value of θ , the weaker is density dependence, and the more it is concentrated at population densities close to the carrying capacity. Typical consequences of increasing the θ value are illustrated in Fig. 3. A value of $\theta < 1$ increases the range of parameters producing mutualism and the magnitude of the mutualism when it occurs, while θ values > 1 have the opposite effect. These simulations suggest that apparent competition is more likely when density dependence is relatively weak (large θ) than when it is strong (small θ). This is consistent with the general result (noted in *When and why does cycling alter apparent competition?*), that prey cannot coexist with a shared predator in the absence of density dependence. However, changing the nature of density dependence has several effects on the dynamics of the system. Increasing density dependence by decreasing θ tends to stabilize the system, and a sufficient increase in stability produces apparent competition. Thus, decreasing θ while not changing other parameters may shift a system from mutualism to competition; e.g., for $D = 0.9$ or 1.0 in Fig. 3. However, if the equilibrium of a one-prey system is unstable, stronger density dependence (smaller θ) tends to make cycle amplitude more sensitive to the addition of a second prey species, and this favors apparent mutualism.

The results for the θ -logistic model also show that the nature of apparent competition or mutualism cannot easily be predicted from the direction of the predator population's response to increased carrying capacity in a one-prey-one predator system. Values of $\theta > 1$ result in reductions in the mean predator density with increasing K (see correction to Abrams and Roth 1994a

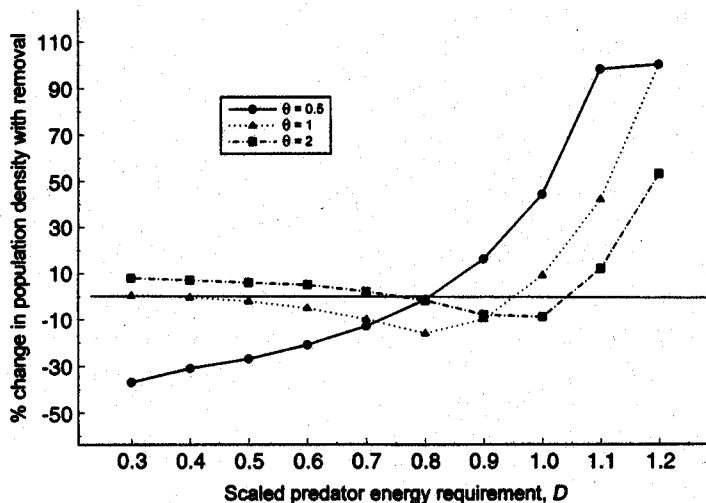
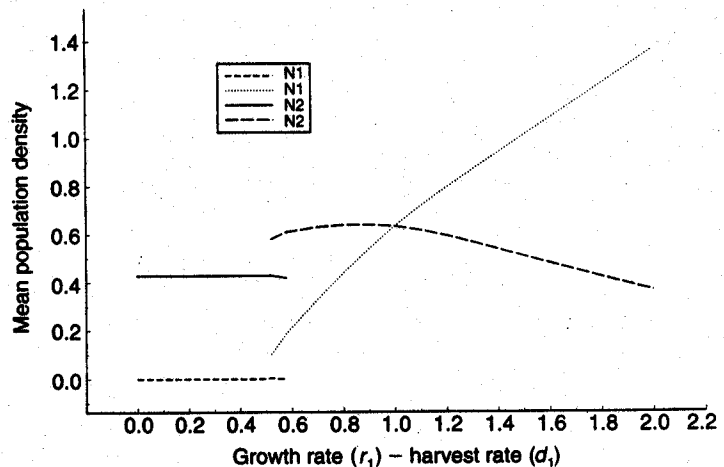


FIG. 3. Proportional changes in population density following removal of a second, equivalent prey population, based on simulations of Eqs. 3 using three values of the density-dependence parameter, θ . The x axis gives different values of the scaled predator energy requirement, D (this is equivalent to the unscaled requirement T for the parameters used here). The horizontal line separates positive values, indicating apparent competition, from negative values, which indicate mutualism. The other parameter values are: $r_1 = 1$, $K_1 = 1$, $C_1 = 5$, $h_1 = 0.6$, $\theta = 1$, $e_1 = 1$. These are equivalent to the scaled parameter values $\alpha = 5$ and $\beta = 3$.

FIG. 4. Results of simulations of Eqs. 3. The responses of mean densities of the two prey species to the per capita harvest rate of prey species 1, d_1 , is shown. Both prey species have intrinsic growth rates $r = 2$, carrying capacities $K = 2$, and capture rates $C = 5$. Prey 2 experiences a per capita harvest of $d_2 = 1$. The other parameters are $e = 1$, $h = 0.6$, and $T = 1.2$. The parameters in the symmetrical system ($r_1 - d_1 = 1$) are equivalent to scaled parameter values $\alpha = 5$, $\beta = 6$, and $D = 0.6$



in Abrams et al. 1997). This fact might suggest that mutualistic relationships between prey should be most likely for such systems. However, the opposite is true; smaller values of θ result in more cases of, and larger magnitudes of mutualism. This occurs in spite of the fact that the mean predator population increases following addition of the second prey species when θ is significantly less than 1 (Abrams et al. 1997). The mutualism occurs because the consequences of greater cycle amplitude following addition of the second prey outweigh the effect of the small change in mean predator density.

Responses of prey density to changes in the mortality rate of the other prey species

The interaction between prey that share a predator cannot be completely understood by considering responses to addition or removal of one of the species. Here we consider the change in density of one prey that occurs when the second prey experiences a change in its per capita mortality rate, d , in Eqs. 3. Fig. 4 illustrates the interspecific effects in a representative case. Here, the two prey are identical except for their per capita mortality; prey species 2 always experiences a mortality rate $d_2 = 1$, but we calculated mean densities of both prey species for harvest rates of species 1 ranging from $d_1 = 2$ ($=r$) down to $d_1 = 0$. Thus, the system is symmetrical when $d_1 = 1$. Species 1 cannot exist when $r_1 - d_1$ is below a threshold value. When $r_1 - d_1$ is just above this threshold, there are two alternative attractors; a stable point with species 1 absent, and a limit cycle with both species present. As $r_1 - d_1$ becomes somewhat larger, the stable point becomes globally unstable; the two leftmost lines in Fig. 4 terminate at this point.

The system is a symmetrical one with two prey when $r_1 - d_1 = 1$ and is a single-prey system (species 2 only) when $r_1 - d_1$ is close to zero. Comparing these two points on Fig. 4 illustrates the mutualism in symmetrical systems discussed above; the mean density of spe-

cies 2 is higher in the two-species system than when it alone is present. However, small or moderate changes in the per capita mortality of one species near the symmetric ($r_1 - d_1 = 1$) equilibrium always result in a competitive effect; increasing (decreasing) $r_1 - d_1$ decreases (increases) the density of species 2. Fig. 4 also shows that there is a positive effect of removing one of the prey species for the remaining prey species in a range of asymmetrical systems. Adding species 1 increases the mean density of species 2 for initial $r_1 - d_1$ (net growth) values ranging from roughly 0.5 to 1.77. If species 1 has a sufficiently higher net growth rate than species 2, however, adding species 1 reduces the mean density of species 2. In all examples of Eqs. 3 that we have simulated, when the two prey species initially have identical growth equations, and the maximum growth rate of one species is increased by a small proportion, the other species decreases. This suggests that the response of one prey species to small changes in the growth rate of the other prey can always be described as apparent competition in this model. However, the change in the mean density of one species caused by a small change in the harvest rate of another species in a cycling system is always less than the change in the equilibrium density; apparent competition is less than would be predicted based on equilibrium densities.

Another complication illustrated in Fig. 4 is that there are often alternative attractors for a range of growth rates close to the minimum that will allow species 1 to exist in the system. In these cases, a very small number of species 1 introduced into the system will go extinct, but a large starting density will result in coexistence of both prey species. Alternative attractors (one limit cycle and one stable point) were observed in many asymmetric systems, often for broader ranges of parameter values than in Fig. 4. Alternative attractors complicate the definition and measurement of interspecific interactions because changing a parameter (such as the maximum growth rate or harvest rate

TABLE 2. Change in the remaining prey species after removing one prey species in asymmetric systems.

| Asymmetric parameter | ΔN_1 after removing species 2 (%) | ΔN_2 after removing species 1 (%) |
|----------------------|---|---|
| C_1 | | |
| 7.5 | +37.9 | -29.7 |
| 3.75 | -9.8 | +21.7 |
| 2.5 | +17.7 | +620.1 |
| h_1 | | |
| 0.8 | -3.7 | -28.0 |
| 0.45 | -22.2 | -4.2 |
| r_1 | | |
| 1.25 | -25.1 | +9.2 |
| 0.75 | +25.2 | -26.0 |
| K_1 | | |
| 0.75 | +5.4 | -14.6 |
| 0.875 | -10.6 | -15.5 |
| 1.25 | -10.5 | -17.2 |
| 1.5 | -6.7 | -18.1 |

Note: Numbers are the percentage change in the original population density, with negative values indicating a decrease (i.e., a positive effect of the removed species on the remaining one). Results are based on Eqs. 3 with $\theta = 1$. Other than the noted asymmetric parameter, each prey species has $r = 1$, $K = 1$, $C = 5$, $h = 0.6$, $d = 0$; the predator has $e = 1$, $T = 0.8$.

of one species) changes both the average densities on each attractor and the sizes of their basins of attraction. Alternative attractors have also been described in ordinary differential equation models of three-species food chains (Rosenzweig 1973, Hastings and Powell 1991, Abrams and Roth 1994a, McCann and Yodzis 1994), and Holt (1977) earlier raised the possibility of alternative equilibria in systems with shared predation.

Other asymmetric systems

It is not possible to explore the full range of parameter space for asymmetric systems. Our approach here was to take some symmetric systems and make them asymmetric by changing a single parameter in species 1. Although this is necessarily an incomplete analysis, all of the results obtained were easily understood based on the principles revealed by symmetric systems. If introducing the second prey species increased the amplitude of cycles, it tended to increase the mean density of the original prey. If introducing the second prey reduced cycle amplitude, it tended to decrease the mean density of the resident prey. This effect via cycle amplitude was combined with the basic effect of apparent competition, which favors species with large r or small C values (Holt 1977). Because of this combination, interactions in asymmetrical systems were frequently (+, -) in terms of effects on density. Table 2 presents the proportional change in the density of one prey following removal of the other, when the prey differ from each other in one of the four parameters, r , K , h , and C . Mutualism is indicated by negative effects on each species of removing the other, while competition implies positive effects of removal. The symmetric system from which the examples in Table 2 are derived exhibits

mutualism; removing either prey produces a 16% decrease in the mean density of the other prey species. The table shows that mutualistic effects occur for a wide range of asymmetries in the carrying capacity or handling time. Substantial differences in the capture rate, C , or the intrinsic growth rate, r , tend to produce (+, -) interactions. In these cases, the large- r or small- C species tends to have a very large advantage in reproducing in the presence of the predator, which has a negative effect on the small- r or large- C species. The main effect of the presence of the inferior (small- r or large- C) species is to increase cycle amplitude and thereby reduce the predator's effect on the superior species. Differences between prey in their carrying capacities K do not produce as large a difference in prey population sizes as do differences in r or C . Differences in handling time alone do not result in any difference between two coexisting prey in their mean or equilibrium densities. Thus, effects of each prey species on the other tend to be more similar when the asymmetry is a difference in K or h ; all such cases in Table 2 represent apparent mutualism, except for $K_1 = 0.75$.

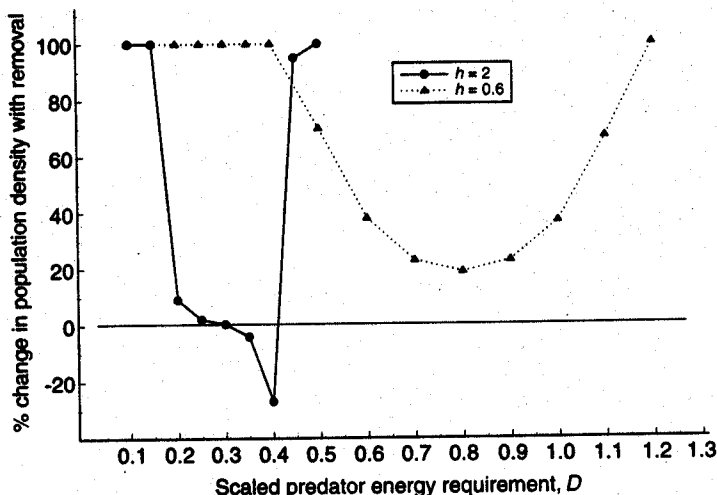
Alternative models

The linearity of the predator's numerical response is important in determining the relationship between prey carrying capacity and mean predator density in single-prey systems (Abrams and Roth 1994a). The nonlinear relationship that we explore here is a predator per capita growth rate given by $B - \delta(1 + \beta N_1 + \beta N_2)/(\alpha(N_1 + N_2))$. In this formula the constant B represents the maximum per capita rate of increase, and the constant δ scales the hyperbolic rate at which the per capita growth rate decreases as food intake rate decreases. We investigated Eqs. 4 with this formula substituted for the predator's per capita growth rate in Eq. 4b, yielding,

$$dP/dt = P[B - \delta(1 + \beta N_1 + \beta N_2)/(\alpha(N_1 + N_2))]. \quad (5)$$

Getz (1993) and Abrams and Roth (1994a) discuss this nonlinear numerical response; it has the property that the predator population declines extremely rapidly when prey are rare. In addition, the growth rate asymptotes rather quickly as prey become common. If the system has a stable point equilibrium, this change in the predator equation does not change equilibrium densities or the extent of apparent competition from a comparable system (with the same α values, β values, and with $B/\delta = 1/D$) based on Eqs. 4. If, however, the system undergoes sustained fluctuations in abundance, this nonlinear numerical response dramatically increases the range of parameters producing apparent mutualism, and increases the magnitude of the mutualism. If, for example, we assume that $\alpha = 5$ and $\beta = 3$ (as in Fig. 1B), and $B = 1$, then the mean prey density of each species in the two-prey system based on Eq. 5 may be almost an order of magnitude larger than that of a single prey, when δ is sufficiently small. This contrasts with a maximum mutualistic effect of <20%

FIG. 5. Interactions between prey when functional responses are type-3. The two lines describe the percentage change in remaining prey after removing one of two equivalent prey species. The results are based on simulations of Eqs. 3 modified by adopting the second of the expressions for the type-3 response in the text. The x axis gives different values of the scaled predator energy requirement, D (this is equivalent to the unscaled requirement T for the parameters used here). The parameter values are $r_i = 1$, $K_i = 1$, $C_i = 5$, $\theta_i = 1$, $e_i = 1$, and $\gamma = 0.05$. One line is based on a handling time of 0.6, and the other has a handling time of 2.0. The horizontal line separates positive values, indicating apparent competition, from negative values, indicating mutualism.



in the analogous system with a linear numerical response (Fig. 1B with $D = \delta$). The underlying reason for the mutualism is again the concave-down shape of the predator's per capita growth rate as a function of prey density. Because of this numerical response, an increased mean prey density must accompany the increased variation that follows from the addition of a second prey species.

Another set of alternative models assumes that the predator has a type-3 functional response. We investigated the two-species versions of a functional response model analyzed by Abrams and Roth (1994a). When a single prey is present, the functional response is $CN^2/(\gamma + N + hCN^2)$, where C and h are the encounter rate and handling time, as before. The parameter γ is a measure of the nonlinearity of this formula at low prey densities; as γ approaches 0, this formula approaches the disk equation, which is approximately linear when prey are rare. In extending this response to systems with two similar prey species, two alternative formulas for the response to prey species i in a two-prey system were examined: (1) $C_i N_i^2 / (\gamma + N_i + C_1 h_1 N_1^2 + C_2 h_2 N_2^2)$, and (2) $C_i N_i (N_1 + N_2) / (\gamma + N_1 + N_2 + (C_1 h_1 N_1 + C_2 h_2 N_2)(N_1 + N_2))$. The first is appropriate when each prey species approaches immunity from predation as its density approaches zero. The second is appropriate when total prey density determines the predator's response, so that both prey species must be rare to produce a large decrease in the predator's foraging (see Abrams 1987c). In either case, a very small value of γ indicates a response that is very similar to type 2. When γ is slightly larger, systems are stable when D is either very small or large, and are unstable for a range of intermediate values. If γ is sufficiently large, systems are stable for all D , and the indirect interaction between prey is always apparent competition (Holt 1983). We therefore examined indirect effects between prey for several intermediate values of γ .

Fig. 5 shows the proportional change in population

density of one prey upon removal of the second for $\gamma = 0.05$, $C_i = 5$, and for two values of h_i ($h_i = 0.6$; equivalent to $\alpha = 5$ and $\beta = 3$ in Fig. 1; $h_i = 2.0$, equivalent to $\alpha = 5$ and $\beta = 10$ in Fig. 1). Mutualism occurred for a range of predator energy requirements, $D (=T)$, in the comparable systems with type-2 functional responses (Fig. 1). This figure assumes that the type-3 functional response is of the second variety, where the predator responds to total prey density. The first variety of type-3 response produced very similar results for these (and most) parameter values, although the magnitudes of mutualistic responses were slightly smaller. Comparing the results for $h = 0.6$ (i.e., $\beta = 3$) in Fig. 5 with the comparable results for type-2 responses in Fig. 1B indicates that having a type-3 response may increase the likelihood of apparent competition between prey when handling times are not very large. However, both type-2 and type-3 responses have similar ranges of parameters producing mutualism when handling times are larger ($h = 2$). Because type-3 responses prevent extremely low prey population densities, persistence of systems with large values of h (or β) and relatively low predator energy requirements, T (or D), becomes more likely than in comparable systems with type-2 responses. Because relatively low energy requirements and high handling times often produce mutualism, the larger range of energy requirements yielding persistence with type-3 responses may make mutualism more common with type-3 responses than with type-2. More and better measurements of handling times and energy requirements in the field would be required to draw a definite conclusion about how the "sigmoidicity" of the functional response affects the likelihood of mutualism. Systems with type-3 responses are stable at very low energy requirements (e.g., caused by very low mortality rates). As a result, they always exhibit apparent competition in these cases, as well as in cases where the predator's energy requirement (D) is very high.

A final alternative that bears mentioning is the presence of more than two prey species. Although this is too broad a topic to consider in detail, we should point out that addition of one prey to a cycling predator-prey system often makes it easier for additional prey to invade the system. Ease of invasion may be measured by the range of r_3 or C_3 values that allow the third species to increase when it is rare and the other two species occupy the attractor (limit cycle or stable point) of the two-prey one-predator system. In the system illustrated in Fig. 2, a second prey species with C , h , and K values equal to species 1 can invade if $r_2 > 0.667$ ($r_1 = 1$). After addition of a second prey with $r_2 = 1$, a third (again with the same C , h , and K) can invade if $r_3 > 0.604$. Additional prey reduce the threshold value of r for invasion still further.

Alternative measures of interspecific effects

We have analyzed effects of the presence or growth rate of one prey on the average density of the other prey species. This is the most common way of summarizing densities in continuously varying systems. However, any single statistic is incapable of characterizing a population undergoing sustained cycles. One statistic that behaves very differently from the mean density is the minimum density. In all systems we have simulated where the predator had a type-2 functional response, addition of a second prey species decreases the minimum value of the first prey species (e. g., Fig. 2). Because low densities increase the risk of extinction in finite populations, it is possible to argue that the indirect effect between prey could be negative even when the presence of one increased the mean population density of the other. However, defining interactions based on effects on minimum population size does not eliminate apparent mutualism, but rather, changes the circumstances where mutualism occurs. Positive interspecific effects on minimum density occur when the predator has a type-3 functional response and the addition of the second prey stabilizes a cycling one-prey system. This same conclusion would hold for effects measured by other population statistics that weight low densities heavily, such as the harmonic mean.

However, it is not clear that minimum density is an appropriate metric for defining interspecific effects. In systems with finite populations, larger amplitude cycles following the addition of a second prey not only increase the chance of extinction of the first prey, but also increase the probability of extinction of the predator. If the latter occurs more frequently than the former, the effect of the second prey on the first would clearly be positive. Regardless of the statistic used to classify interspecific effects, the possibility of alternative attractors and the dependence of the sign of an effect on the magnitude of perturbation further complicate the classification of interactions.

DISCUSSION

The most general conclusion from the preceding analysis is that two pieces of information are of overriding importance in assessing interactions in systems with shared predation that lack a stable equilibrium point: (1) the effect of adding, removing, or modifying a prey species on the shape of population fluctuations; and (2) the nature of the nonlinearity in the relationship between prey density and predator per capita growth rate. The latter is composed of the functional and numerical responses. It is not widely appreciated how dramatically changes in the shape of population cycles can affect mean population densities in this and other simple community models.

It is difficult to draw conclusions about the likelihood of mutualism between shared prey in nature based on the frequency of occurrence of mutualism in the simplified models considered here. We do not know enough about the nonlinearity of functional and numerical responses and of prey density dependence to estimate the probability of competition vs. mutualism. Regardless of whether mutualism occurs, cycling always reduces the extent of apparent competition when the predator's per capita growth rate is a concave function of prey density. If neither the predator's functional nor its numerical response is highly nonlinear, the interaction between prey is expected to be apparent competition, even when there are large-amplitude cycles. The largest magnitudes of apparent mutualism (or the smallest magnitudes of apparent competition) occur when there are major differences between the properties of the cycles in one- and two-prey systems. In many cases, different magnitudes of change in the growth parameters of one prey species can have opposite effects on the mean density of the second species, and effects between prey with significantly different growth functions can be (+, -) in sign.

Although the cycles discussed here were all produced by nonlinearity in the predator's functional response, this is not a necessary condition for cycles to reduce or reverse apparent competition. Seasonal variation in prey growth rates can produce the same effect, provided the predator has a saturating numerical response. Addition of a second prey species in such a case increases the amplitude of population cycles, provided that prey respond similarly to the environmental seasonality. Larger cycles again reduce apparent competition or produce mutualism or (+, -) effects (P. A. Abrams, *unpublished manuscript*). It is also possible for time-lags or Allee effects in the prey's population growth to result in cycles (e.g., Gilpin 1975), which again can produce mutualism given a sufficiently nonlinear predator growth function.

The possibility of mutualistic interactions between prey that share predators is not unique to systems with sustained population cycles. If the predator has some form of density dependence in its growth rate due to

factors other than prey consumption, then interactions between prey can be mutualistic in stable systems that are otherwise similar to those considered here (Holt 1977, 1987, Holt and Kotler 1987, Abrams and Matsuda 1996). Mutualism in such systems is most likely when the predator's energy requirement (D or T) is small, and becomes less likely when the energy requirement is large. We have not systematically explored the interactions between shared prey when there is both cycling and non-prey-related density dependence in predator growth. However, the simulations we have done suggest that typically, very low predator energy requirements lead to stable systems with apparent mutualism between prey; large requirements lead to stable systems with apparent competition; and intermediate requirements may result in limit cycles with either competitive or mutualistic interactions between prey. As Abrams and Matsuda (1996) point out, very little is known about the extent of non-prey-related density dependence among predators in natural systems. Abrams (1987a) presents another possible mechanism for mutualistic interactions between shared prey based on adaptive risk-taking by the prey while foraging. Under this scenario, increased predator density caused by a positive perturbation to one prey species can increase the equilibrium density of the second prey species, by forcing it to reduce its overexploitation of its own resource.

The multiplicity of mechanisms for mutualism between shared prey species makes it surprising that well-documented field examples have apparently not been described. Here we can only speculate about the reason for this lack of experimental evidence. There has been a tendency for common ecological phenomena to be overlooked or misinterpreted in the absence of a well-known body of theory. Comparing the meager experimental evidence cited in Holt's original (1977) article on apparent competition with the large body of evidence reviewed 17 yr later (Holt and Lawton 1994) is an excellent illustration of this tendency. The only current evidence for positive indirect effects between prey comes from short-term studies that did not involve a numerical response by predators (Holt and Lawton 1994).

The possibility of apparent mutualism suggests that predation need not be a force that limits species diversity on a lower trophic level. For a wide range of parameters in several of the models we have studied, adding a prey species makes it easier for subsequent prey to invade, provided that they do not compete for resources with the resident species (Holt 1996). This also occurs when the predator population is limited by some resource other than prey, and has a saturating functional response (Abrams and Matsuda 1996).

It should not be difficult to examine the indirect interactions between prey in cycling systems in the laboratory. Experiments on protist predator-prey systems from Gause (1971) to Morin and Lawler (1995) have

shown that sustained fluctuations are common and that interspecific interactions can be quantified in systems with several species. Luckinbill (1973) demonstrated that stability of protist predator-prey systems could be manipulated by changing the viscosity of the medium or the input rate of the prey's food. Such systems could be used to experimentally explore indirect effects in unstable communities.

To our knowledge, indirect effects have not been studied in field systems that exhibit cycles. Field experiments, particularly those involving long-lived organisms, are more difficult. However, it should often be possible to measure aspects of those systems that are major determinants of the nature of indirect effects in cycling systems. This study has shown that there are several aspects of predator-prey models that are important in determining indirect effects between prey, but which are very poorly understood in natural systems. There has been relatively little study of, and apparently no review articles on, the numerical responses of predators. The importance of the numerical response in determining the nature of the indirect interaction between shared prey argues for a much greater attention to this topic. We are also almost totally ignorant of the factors that are important in causing cycles in either laboratory or field systems in which cycles have been observed (McCauley and Murdoch 1987, Harrison 1995). Significant saturation in the predator functional response can generate apparent mutualism under many conditions. At least some functional response measurements (Abrams et al. 1990, Messier 1994) demonstrate very sharply saturating responses.

The present results also call for additional theoretical work. There are a variety of ways in which the models considered here could be extended. We have assumed that the system is closed and homogeneous, except for some limited consideration of immigration of one prey, and work on metapopulation systems is required (but see Holt 1984, 1996). Variability, whether exogenous or endogenous, has often been regarded as a factor that decreases the strength of interactions between species. In fact, variability need not weaken interactions, and can have a rich and varied array of influences on how species affect each other. We still understand very few of these influences. Shared predation is only one of an infinite range of indirect interactions that are possible in natural communities (Abrams et al. 1996); understanding the consequences of population fluctuations in all such systems is a task for the future.

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