

The influence of vigilance on intraguild predation

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Abstract

Theoretical work on intraguild predation suggests that if a top predator and an intermediate predator share prey, the system will be stable only if the intermediate predator is better at exploiting the prey, and the top predator gains significantly from consuming the intermediate predator. In mammalian carnivore systems, however, there are examples of top predator species that attack intermediate predator species, but rarely or never consume the intermediate predator. We suggest that top predators attacking intermediate predators without consuming them may not only reduce competition with the intermediate predators, but may also increase the vigilance of the intermediate predators or alter the vigilance of their shared prey, and that this behavioral response may help to maintain the stability of the system. We examine two models of intraguild predation, one that incorporates prey vigilance, and a second that incorporates intermediate predator vigilance. We find that stable coexistence can occur when the top predator has a very low consumption rate on the intermediate predator, as long as the attack rate on the intermediate predator is relatively large. However, the system is stable when the top predator never consumes the intermediate predator only if the two predators share more than one prey species. If the predators do share two prey species, and those prey are vigilant, increasing top predator attack rates on the intermediate predator reduces competition with the intermediate predator and reduces vigilance by the prey, thereby leading to higher top predator densities. These results suggest that predator and prey behavior may play an important dynamical role in systems with intraguild predation.

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1. Introduction

Intraguild predation (IGP) occurs when a consumer kills an interspecific consumer within its own guild (Polis et al., 1989). Usually, IGP occurs when a top predator kills and consumes an intermediate predator with which it also shares a prey resource. IGP occurs very frequently in nature (Arim and Marquet, 2004), including many guilds of mammalian carnivores (Rosenzweig, 1966). Reviewing the literature, Palomares and Caro (1999) found 97 pairwise interactions between mammalian carnivores, with 27 top predator species killing 54 intermediate predator species. For example, cheetah cubs (*Acinonyx jubatus*) are killed by spotted hyenas (*Crocuta crocuta*) and leopards (*Panthera pardus*), while both cheetah cubs and adults are killed by lions (*Panthera leo*; Laurenson, 1995; Schaller,

1972). Interestingly, however, Palomares and Caro (1999) found that of the 21 top predators for which information was available, the top predator species always totally or partially ate their intraguild victims in only 10 cases, sometimes ate them in eight cases, or never ate their victims in three cases. Thus, roughly half of these top predator species that kill intermediate predator species rarely or never consume their victim. For example, spotted hyenas almost always consume the cheetahs they have killed, but leopards only occasionally consume cheetahs, and lions are believed to never consume the cheetahs they have killed (Laurenson, 1995; Palomares and Caro, 1999; Schaller, 1972).

This raises a problem: IGP theory of two predator species sustained by a single prey resource predicts that such a system will be stable only if the intermediate predator is better at exploiting the shared prey than the top predator, and the top predator also gains significantly from consumption of the intermediate predator (Borer et al.,

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2003; Holt and Polis, 1997; Křivan and Diehl, 2005). The examples of Palomares and Caro (1999) suggest that in some cases mammalian top predator species kill but rarely consume intermediate predator species, and there is no indication that any of these interactions are unstable. To begin reconciling theory to observation, we start by considering why some mammalian predators go to the trouble of killing other predators and then not consuming them.

If a top predator kills an intermediate predator, but does not consume it, the only gain the top predator can expect to enjoy is via a shift in the abundance or availability of the shared prey. By removing a competitor, there could be future gains to a top predator (or possibly its kin) through increasing prey numbers. Although most mammalian carnivores do not specialize on a single prey species, the potential for interspecific competition is still significant (Eaton, 1979; Rosenzweig, 1966). For instance, Caro and Stoner (2003) used range maps of carnivore species in Africa to suggest that mammalian carnivores in Africa may share food resources with an average of 22 other mammalian carnivore species.

Exploitative competition may not be the only process by which killing a competitor is important, however—vigilance levels of both the intermediate predator and the shared prey may be affected. If individual prey are vigilant, eliminating the intermediate predator could benefit the top predator by indirectly relaxing vigilance in the shared prey. Additionally, if eliminating individual intermediate predators makes others of that species more vigilant, and there is a tradeoff between vigilance and exploitative abilities, the intermediate predator may become a less efficient competitor for the prey, again benefiting the top predator.

Prey vigilance has been observed to be important for predator–prey interactions in a number of mammalian systems (FitzGibbon, 1989, 1990; Hunter and Skinner, 1998; Laundre et al., 2001). One consequence of prey vigilance is that prey have a reduced food intake rate because vigilance interferes with foraging (Fortin et al., 2004; Illius and FitzGibbon, 1994), but predators also have a reduced food intake rate due to the decrease in prey vulnerability (FitzGibbon, 1989).

There is less direct evidence for top predator species inducing vigilance behavior in mammalian intermediate predator species. Durant (2000) found, however, that cheetahs listening to playbacks of lion vocalizations are much less likely to hunt after hearing the playback, and often move away from the area of the playback. Thus, vigilance by the intermediate predator to predation from a top predator may reduce its efficiency in hunting a shared prey species.

There are interesting questions about how systems with a top predator that kills but does not consume an intermediate predator may evolve, but in this paper we focus on the ecological issue of how such seemingly wasteful behavior alters the dynamical interactions among predators and prey in a multispecies setting.

2. Methods

Previous models have analyzed the affect of optimal foraging behaviors by the top predator on systems with IGP (Křivan, 2000; Křivan and Diehl, 2005), but none have examined the impact of vigilance. We use differential equation models to investigate IGP when top predators rarely or never consume intermediate predators. We begin by allowing the top predators and intermediate predators to share a single prey resource. In one model we assume that only the prey is vigilant; in a second model we assume that only the intermediate predator is vigilant. It is useful to consider these two models, which permit us to determine the impact of vigilance by one species, independently of vigilance by the other species. Finally, we increase the complexity of the models by allowing the top predator and intermediate predator to consume two species of shared prey, again assuming either that both prey species are vigilant or that only the intermediate predator is vigilant. (We intend in the future to examine systems where all species are potentially vigilant.)

Brown et al. (1999) have suggested that resource vigilance is a stabilizing influence in communities comprised of specialist predator–prey interactions. When consumer density is high, prey vigilance is also high, preventing the consumer from over-exploiting its resource. Conversely, when consumer density is low, prey vigilance is also low, allowing prey to be more easily caught and thereby increasing consumer growth rate. Similarly, Fryxell and Lundberg (1998) found that optimal allocation of foraging time by a prey species to gathering its resource (as a means of balancing foraging intake with the risk of predation) also acted to increase the stability of predator–prey dynamics. Based on these previous results, we hypothesized that prey or intermediate predator vigilance could help stabilize mammalian carnivore systems with IGP where top predators rarely or never consume those intermediate predators that they kill.

2.1. One shared prey species and vigilant prey

We begin with a model that tracks densities of a top predator, P , intermediate predator, N , and a single shared prey, R . We initially assume that the prey is vigilant, but that the level of vigilance, v_R , is fixed and does not vary with top predator, intermediate predator, or prey density. This provides an essential baseline for then examining the impact of labile vigilance. The model is based on a simple Lotka–Volterra formulation similar to that used by Holt and Polis (1997) to model IGP, but incorporates prey vigilance with a tradeoff by decreasing the growth rate of the prey with increasing vigilance, while also decreasing the attack rate of the top and intermediate predators with increasing vigilance (following Brown et al., 1999). The model is as follows:

$$\frac{dP}{dt} = P(b'a'R + \beta\alpha N - m'),$$

$$\begin{aligned}\frac{dN}{dt} &= N(baR - m - \alpha P), \\ \frac{dR}{dt} &= R \left[(1 - v_R)r \left(1 - \frac{R}{K} \right) - d'P - aN \right],\end{aligned}\quad (1)$$

where d' and a are the attack rates of the top predator and intermediate predator on the prey, respectively. The attack rates are assumed to decline with prey vigilance as

$$\begin{aligned}d' &= \frac{c'_R}{l'_R + g'_R v_R}, \\ a &= \frac{c_R}{l_R + g_R v_R}.\end{aligned}\quad (2)$$

The attack rates are influenced by the ability of prey vigilance to reduce predation, and are based on the expression for attack rate used previously by Brown et al. (1999) in a one predator–one prey model. The rest of the parameters in Eqs. (1) and (2) are as follows: r is the intrinsic growth rate of the prey, and K is its carrying capacity; m' and m are the density-independent mortality rates of the top and intermediate predators; and b' and b scale prey consumption to reproduction for the top and intermediate predators. The top and intermediate predator encounter rates with the prey are denoted by c'_R and c_R , the quantities g'_R and g_R are the abilities of vigilance to reduce predation, and finally, $1/l'_R$ and $1/l_R$ are the lethality of the top and intermediate predators on the prey in the absence of vigilance. In Eq. (1), vigilance affects prey growth rate when prey are rare, but does not influence prey carrying capacity. From the prey's perspective, there is a tradeoff between its maximal growth rate, and its ability to escape predation. Finally, α is the mortality inflicted on the intermediate predator by the top predator, and β scales the conversion of intermediate predator consumption to top predator reproduction.

We can decompose β into two parameters: the probability that the top predator will eat an intermediate predator that it has killed, and the conversion of energy gained from eating an intermediate predator by a top predator to its reproduction. In this paper, we will assume that the conversion of energy gained from eating the intermediate predator is constant, thus when we vary β , we change the probability that the top predator will eat a given intermediate predator that it has killed. As shorthand, we refer to β as 'consumption' of the intermediate predator by the top predator. Consequently, we are interested in independently varying α and β between zero and one to determine how the mortality and consumption of the intermediate predator by the top predator influences the stability of the system. We will be particularly interested in the case of small β , approaching zero, which seems a feature of the natural IGP systems discussed above.

In model (1), we assumed that the top predator and intermediate predator differed only in the ability of prey vigilance to reduce their predation rates ($g'_R > g_R$). We thus assumed that vigilance reduced predation by the top predator more efficiently than by the intermediate predator.

This assumption results in the attack rate of the top predator on the prey being lower than the attack rate of the intermediate predator on the prey ($d' < a$). The assumption that prey vigilance reduces predation by the top predator more efficiently than by the intermediate predator is biologically reasonable because the intermediate predator is a specialist on the prey, while the top predator is a generalist on both the intermediate predator and the prey. Consequently, the intermediate predator likely faces greater selection pressure than the top predator to be less affected by prey vigilance. The prey, on the other hand, faces selection pressure for vigilance to prevent attack from both the top and intermediate predators. Therefore, we assume that prey vigilance reduces predation by the top predator more efficiently than by the intermediate predator. This argument may not hold if the top predator does not consume the intermediate predator ($\beta = 0$) because the top predator is then no longer a generalist. However, as we show in the Results section, this point is moot because coexistence of the system does not occur when $\beta = 0$. Unfortunately, we know of no empirical studies that we can use to test these assumptions.

Note also that when vigilance reduces predation by the top predator less efficiently than by the intermediate predator ($g'_R < g_R$), the intermediate predator is excluded from the system. This occurs because the top predator can kill the intermediate predator, but the top predator is also better at attacking the prey; as a result, the top predator drives the intermediate predator extinct. In order to analyze a system with the possibility of coexistence in this paper, we therefore assume that $g'_R > g_R$. We provide a further graphical examination of the affect of the g_R parameters on model (1) in Appendix A, as well as a graphical examination of how prey carrying capacity, K , influences coexistence in model (1) (Křivan, 2000; Křivan and Diehl, 2005). Understanding how prey productivity affects IGP is an interesting and important issue, but is tangential to the main theme of our paper.

2.2. One shared prey species and vigilant intermediate predators

We next model an IGP system with one shared prey, but with a vigilant intermediate predator. The model is

$$\begin{aligned}\frac{dP}{dt} &= P(b'd'R + \beta\alpha N - m'), \\ \frac{dN}{dt} &= N[(1 - v_N)baR - m - \alpha P], \\ \frac{dR}{dt} &= R \left[r \left(1 - \frac{R}{K} \right) - d'P - (1 - v_N)aN \right],\end{aligned}\quad (3)$$

where a and d' are now constants, but α declines with vigilance as follows:

$$\alpha = \frac{c_N}{l_N + g_N v_N}.\quad (4)$$

Here, v_N is the vigilance level of the intermediate predator, c_N is the top predator encounter rate with the intermediate predator, g_N is the ability of intermediate predator vigilance to reduce predation, and finally, $1/l_N$ is the lethality of the top predator on the intermediate predator in the absence of vigilance. For the intermediate predator, there is a tradeoff between conversion of captured prey to new predators, and exposure to the top predator. Using model (3), we vary c_N and β between zero and one to determine how the encounter rate of the top predator with the intermediate predator, and the consumption of the intermediate predator by the top predator, influence the stability of the system. We vary c_N instead of α because in model (3) α is dependent on vigilance, which is determined by the intermediate predator, whereas c_N is assumed to be determined solely by the behavior of the top predator. All other parameters are the same as in model (1).

We used models (1) and (3) to find the equilibria when all three species were present, and performed a standard local stability analysis on those equilibria. We used the equilibria to determine how the level of fixed vigilance by the prey or the intermediate predator influenced the density of each species, and whether stable coexistence could occur at low top predator attack rates on, or consumption of, intermediate predators. Formally, when prey or intermediate predator vigilance is fixed, models (1) and (3) are the same as the one explored in Holt and Polis (1997) with a reinterpretation of parameters. This provides a baseline for assessing the consequences of dynamic vigilance.

2.3. Models with dynamic vigilance

Next, we allowed prey vigilance and intermediate predator vigilance to vary dynamically by finding the instantaneous optimal vigilance level, v_R^* or v_N^* , that balanced prey growth rate with top predator and intermediate predator attack rates, or, intermediate predator growth rate with top predator attack rate, respectively (see Appendix B for more details). In effect, this protocol assumes predator and prey numbers stay fixed on a time-scale permitting the prey or the intermediate predator to optimally adjust their vigilance, balancing growth against the risk of predation. Behaviors thus equilibrate adaptively and more rapidly than do population sizes. If the optimal vigilance level of the prey or intermediate predator was less than zero, v_R^* or v_N^* was set equal to zero. Our formulation of optimal vigilance assumed no spatial or patch dynamics (e.g., movement in and out of refuges), and also no direct intraspecific interaction except for direct density dependence in basal prey growth.

With optimal dynamic vigilance, we again found the equilibria for both models when all three species were present. As the value for optimal vigilance depends on the densities of the prey and two predator species, and the densities of the prey and two predators in turn depend on the optimal vigilance, equilibrium values for optimal vigilance and prey and predator densities were determined

by numerical integration and simulation in *Mathematica* (Wolfram Research Inc., 2001).

For model (1), we determined which combinations of top predator attack rates and top predator consumption rates of the intermediate predator allowed stable coexistence of the system. In model (3), we examined how the top predator encounter rate with the intermediate predator and top predator consumption rate of the intermediate predator allowed stable coexistence. We used these results to understand how dynamic vigilance could lead to different population and community level effects than are observed with fixed vigilance.

2.4. Two shared prey species

The IGP model explored by Holt and Polis (1997) assumes that two predator species share just a single limiting prey resource. We increased the complexity of our models by allowing the top and intermediate predators to share two non-competing prey species. Most of the carnivore systems reviewed in Palomares and Caro (1999) feed on multiple prey species, so this is a sensible generalization of the models considered in Holt and Polis (1997). We were inspired by the lion and cheetah interaction mentioned in the Introduction. Lions kill but rarely or never consume cheetah adults and cubs, and lions and cheetahs also share several prey species. Among the shared prey species, wildebeest often make up the largest portion of the lion's diet, and Thomson's gazelle make up a much smaller part of their diet (Schaller, 1972). Conversely, Thomson's gazelle make up most of the cheetah's diet, with wildebeest making up a smaller part of their diet (Caro, 1994). Thus, in our final models, two prey species make up a part of each predator species' diet, but each predator species has a different 'preferred' prey species on which it has a higher attack rate.

In our model, the top predator was assumed to have a low attack rate on prey species 1, and a high attack rate on prey species 2; conversely, the intermediate predator had a high attack rate on prey species 1, and a low attack rate on prey species 2. The predators were thus assumed to show a degree of niche partitioning. In general, such niche partitioning should facilitate predator coexistence, and the presence of additional prey species permits vigilance to occur in more complex ways. We again allowed either the prey or the intermediate predator in turn to be vigilant so that we could determine the effect vigilance at each level had on system stability. The equations incorporating prey vigilance are

$$\begin{aligned} \frac{dP}{dt} &= P(b'_1 a'_1 R_1 + b'_2 a'_2 R_2 + \beta \alpha N - m'), \\ \frac{dN}{dt} &= N(b_1 a_1 R_1 + b_2 a_2 R_2 - m - \alpha P), \\ \frac{dR_i}{dt} &= R_i \left[(1 - v_{R_i}) r_i \left(1 - \frac{R_i}{K_i} \right) - a'_i P - a_i N \right] \quad (i = 1, 2). \end{aligned} \quad (5)$$

Here, all variables are as in model (1), except the subscripts refer to either prey one or prey two. The attack rates of the top predator and intermediate predator on the prey are denoted a'_i and a_i , respectively ($i = 1, 2$) and have the following form:

$$\begin{aligned} a'_i &= \frac{c'_{R_i}}{l'_{R_i} + g'_{R_i}v_{R_i}}, \\ a_i &= \frac{c_{R_i}}{l_{R_i} + g_{R_i}v_{R_i}}. \end{aligned} \quad (6)$$

The corresponding model with intermediate predator vigilance is

$$\begin{aligned} \frac{dP}{dt} &= P(b'_1 a'_1 R_1 + b'_2 a'_2 R_2 + \beta \alpha N - m'), \\ \frac{dN}{dt} &= N[(1 - v_N)(b_1 a_1 R_1 + b_2 a_2 R_2) - m - \alpha P], \\ \frac{dR_i}{dt} &= R_i \left[r_i \left(1 - \frac{R_i}{K_i} \right) - a'_i P - (1 - v_N) a_i N \right] \quad (i = 1, 2). \end{aligned} \quad (7)$$

Here, all variables are as in model (3), the a_i and a'_i are constants, and α is the same as in Eq. (4).

We examined models (5) and (7) by first assuming that the prey species and the intermediate predator had fixed vigilance; this is the model of Holt and Polis (1997) with the parameters re-interpreted to include fixed vigilance and generalized to two prey species. (Holt and Huxel, in press, also explore the impact of multi-prey species in IGP in more detail, but without explicitly considering vigilance). We then explored the models assuming that both prey species or the intermediate predator had dynamic vigilance. When species had dynamic vigilance, vigilance was determined in the same way as before, by finding the instantaneous optimal vigilance level that balanced growth rate to changes in top predator, intermediate predator, and prey densities. We used model (5) to find equilibrium values where all four species were present over a range of top predator attack rates on, and consumption of, the intermediate predator. Similarly, we used model (7) to find equilibrium values over a range of top predator encounter rates with, and consumption of, the intermediate predator. We then determined how killing the intermediate predator—but not consuming it—tended to impact the density of the top predator.

3. Results

We found that vigilance does impact the stability and dynamics of predators and prey in systems with IGP. Local stability analysis shows that a top predator and an intermediate predator sharing one prey species can coexist stably over a wide range of α and β values, with qualitatively similar patterns for fixed and dynamic vigilance. As expected from earlier results (Holt and Polis, 1997), a low top predator consumption rate of the intermediate predator can allow stable coexistence, but to

be stable it requires a high top predator attack rate on the intermediate predator.

3.1. One shared prey species and vigilant prey

In Fig. 1A, the solid lines define the parameter conditions under which the top predator can invade the system. The shaded sections indicate the regions of coexistence of the system. For prey with fixed vigilance, if we assume the intermediate predator can exist in the system in the absence of the top predator, the invasibility condition for the top predator can be derived by finding the equilibrium for the prey and intermediate predator when the top predator is absent, and then solving to find the top predator consumption rate of the intermediate predator that makes the per capita growth rate of the top predator greater than zero. The invasibility condition for the top predator is

$$\beta > \frac{c_R \left(m' - \frac{b' c'_R m (l_R + g_R v_R)}{b c_R (l'_R + g'_R v_R)} \right)}{r \alpha (1 - v_R) (l_R + g_R v_R) \left(1 - \frac{m (l_R + g_R v_R)}{b c_R K} \right)}.$$

When vigilance is fixed, increasing vigilance levels decrease the parameter space over which stable coexistence occurs. This happens because the top predator is less efficient at attacking prey than is the intermediate predator; therefore, increasing prey vigilance requires the top predator to have a higher α or β to remain in the system.

When prey have dynamic vigilance, the optimal level of vigilance tends to be intermediate between zero and one ($v_R^* \sim 0.45$ in Fig. 1A). As a result, the region of coexistence for the system is smaller than when fixed prey vigilance is relatively low ($v_R = 0.1$ in Fig. 1A), but larger than when fixed vigilance is relatively high ($v_R = 0.7$ in Fig. 1A). Dynamic prey vigilance allows the top predator to have a low consumption rate of the intermediate predator, as long as the attack rate on the intermediate predator is high. However, permitting prey to rapidly shift vigilance levels in an optimal fashion does not, by itself, permit persistence of a top predator that gains nothing from the intermediate predator.

When prey are not vigilant ($v_R = 0$), stable coexistence does not occur for the set of parameters in Fig. 1A over any combination of α and β values between zero and one. This occurs because with no vigilance, the top predator and the intermediate predator are assumed to have equal attack rates on the prey, but the top predator also consumes the intermediate predator, thus the top predator drives the intermediate predator extinct. It may appear counter-intuitive that the lower bound of α and β values allowing coexistence moves left and down as vigilance decreases, appearing to increase the range of parameters over which coexistence occurs, but then coexistence does not occur

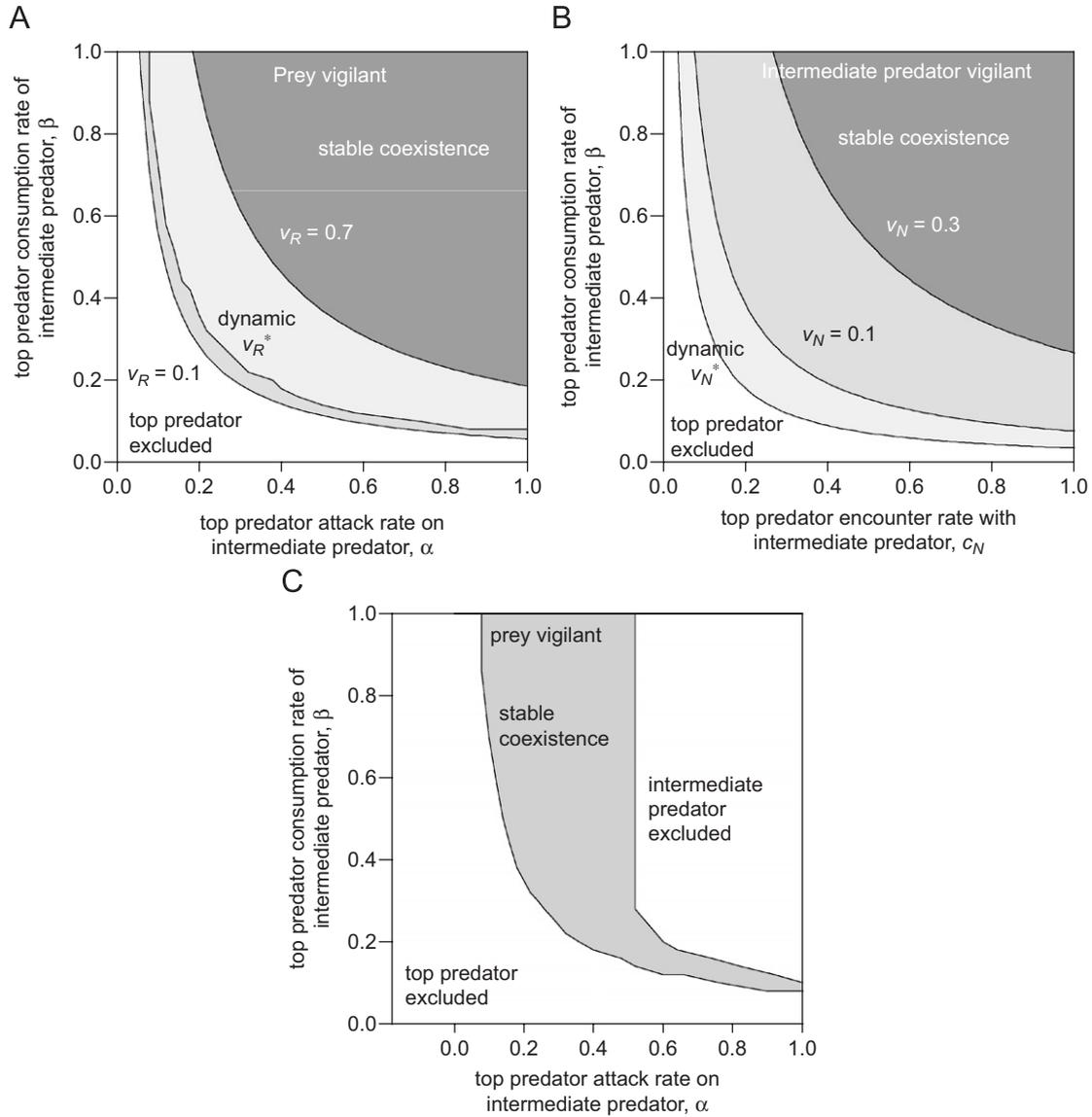


Fig. 1. Regions of locally stable coexistence when the top predator and intermediate predator share one prey species: (A) the prey is vigilant. Coexistence is shown for a range of top predator attack rates on, and top predator consumption rates of, the intermediate predator. The regions of coexistence are shown for fixed vigilance $v_R = 0.1$, dynamic optimal vigilance (v_R^*), and fixed vigilance $v_R = 0.7$. The region of coexistence for a given vigilance begins at its solid line, and extends to all α and β values to the right of the line. Parameters are $r = 1$, $K = 1$, $b = b' = 1$, $m = m' = 0.1$, $c_R = c'_R = 1$, $l_R = l'_R = 1$, $g_R = 10$, and $g'_R = 100$. (B) The intermediate predator is vigilant. Coexistence is plotted over a range of top predator encounter rates with, and top predator consumption of, the intermediate predator. The regions of coexistence are for dynamic optimal vigilance (v_N^*), fixed vigilance $v_N = 0.1$, and fixed vigilance $v_N = 0.3$. The region of coexistence for a given vigilance begins at its solid line, and extends to all c_N and β values to the right of the line. Parameters are $l_N = 1$, $g_N = 10$, $a = 0.167$, $a' = 0.02$. All of the other parameter values as in A. (C) The prey is vigilant. The equation for prey density has been changed from A, so that vigilance reduces the intrinsic prey growth rate but does not reduce prey density dependence. The region of coexistence is shown for dynamic vigilance. All parameters as in (A).

over any parameter values when vigilance is zero. In fact, there is an upper bound for values of α and β above which intermediate predators are excluded, and this bound moves left and down as prey vigilance decreases. The bound occurs at very large values of α and β for the levels of vigilance shown in Fig. 1A, and because we were interested in examining the system at small α and β values, we did not show this bound in Fig. 1A. However, when the vigilance level is very low, the upper bound is near the lower bound, and coexistence occurs over a relatively small region of parameter space. When there is no vigilance, the two

bounds meet and coexistence does not occur over any values of α and β .

3.2. One shared prey species and vigilant intermediate predators

We next examine the case when the intermediate predator is vigilant, for both fixed and dynamic vigilance, and perform a local stability analysis over a range of c_N and α values (Fig. 1B). In both models, coexistence requires some consumption of the intermediate predator by the top

predator, although this consumption can be relatively small if vigilance levels are low. The invasibility condition for the top predator when the intermediate predator has fixed vigilance is given by the equation

$$\beta > \frac{a(1 - v_N)(l_N + g_N v_N) \left(m' - \frac{a'b'm}{ab(1 - v_N)} \right)}{rc_N \left(1 - \frac{m}{abK(1 - v_N)} \right)}$$

When the intermediate predator has dynamic vigilance and the top predator is attempting to invade the system (and therefore has low numbers), the optimal vigilance level is zero. As a consequence, the invasibility condition for the top predator when the intermediate predator has dynamic vigilance becomes

$$\beta > \frac{al_N \left(m' - \frac{a'b'm}{ab} \right)}{rc_N \left(1 - \frac{m}{abK} \right)}$$

Similar to the results found for vigilant prey, when intermediate predators are vigilant, increasing intermediate predator vigilance decreases the parameter space over which stable coexistence occurs. When the intermediate predator's vigilance increases, the top predator must have a higher value of c_N or β to profit from the intermediate predator as before, and thereby remain in the system. Stable coexistence can occur in this example, however, when the intermediate predator is not vigilant ($v_N = 0$) because we have assumed that the top predator still has a lower attack rate on the shared prey than does the intermediate predator. Along the line of dynamic intermediate prey vigilance indicating the region of coexistence, the optimal vigilance level is zero. The optimal intermediate predator vigilance level increases within the region of coexistence.

When predators share a single prey species, prey vigilance and intermediate predator vigilance can be either stabilizing or destabilizing. When prey have either fixed or dynamic vigilance, and values of α or β are small, prey vigilance may prevent the top predator from consuming enough prey, thereby leading to exclusion of the top predator from the system. Conversely, when α or β are large, prey vigilance can keep the top predator from reaching a high enough density that they drive the intermediate predator extinct. Similarly, when intermediate predators are vigilant and top predators have small c_N and β values, vigilance prevents the top predator from consuming enough intermediate predators to remain in the system. Conversely, when c_N and β are large, vigilance can keep the intermediate predator from being over-exploited.

3.3. Different assumption for prey dynamics

In the model with prey vigilance Eq. (1), we assumed that increasing vigilance not only reduced the intrinsic growth

rate of the prey, but also reduced the density dependence experienced by the prey (in effect, we assumed that individual prey face less competition from more vigilant conspecifics). To explore the consequences of making this assumption about the impact of vigilance on density dependence, we again examined the IGP model containing prey with dynamic optimal vigilance Eq. (1), but with a different equation for prey dynamics ($dR/dt = R[(1 - v_R)r - (r/K)R - a'P - aN]$) that allowed vigilance to reduce the intrinsic prey growth rate, but not density dependence. We found that the coexistence of the system for low α or β values was nearly identical to Fig. 1A, with top predators going extinct at very low α or β values (Fig. 1C). In contrast to Fig. 1A, however, when vigilance did not influence prey density dependence, the intermediate predator went extinct at high α and β values (Fig. 1C). If prey do not experience less density dependence as they become more vigilant, they have lower equilibrium densities, which prevents the intermediate predator from coexisting with the top predator at high top predator attack rates, and consumption rates, of the intermediate predator.

3.4. Optimal vigilance levels for prey

When values of β are low in model (1), and the prey are dynamically vigilant, the top predator equilibrium density increases, and the intermediate predator equilibrium density decreases, with increasing α . One might expect decreasing intermediate predator densities to result in decreasing optimal prey vigilance. The reverse is actually found when the full model is examined—optimal vigilance *increases* with decreasing intermediate predator densities. In Appendix C we explore how the density of each species in the system influences the optimal vigilance of the prey or intermediate predator. The reason that optimal prey vigilance increases with decreasing intermediate predator density is because as intermediate predator density decreases, prey density increases, and prey vigilance increases with prey density (Appendix C).

It may seem counterintuitive that prey vigilance increases with prey density. This occurs because at high prey densities, there is little opportunity for prey fecundity due to density dependence (given the assumption about the tradeoff between vigilance and maximal growth rate in Eq. (1)). As a consequence, at high density, the optimal prey behavior is to spend most of its time vigilant (McNamara and Houston, 1992; Repasky, 1996). As shown in Appendix B, as prey density increases, the fitness curve for the prey as a function of vigilance flattens out, making each new increment of vigilance less costly for the prey. This may appear at odds with empirical studies that find that vigilance decreases with group size (reviewed in Caro, 2005; Krause and Ruxton, 2002). However, in our model, we are not assuming that prey form groups; we assume that prey are solitary organisms. Future work incorporating

prey group behavior into a system with prey vigilance and IGP may yield interesting results.

The result of prey vigilance increasing with prey density is that as α increases, top predator density increases, but prey vigilance also increases. As a consequence, for one shared prey species, increasing top predator attack rates on the intermediate predator does not lower prey vigilance—it instead *increases* vigilance.

3.5. Two shared prey species

When we assume that the top predator and intermediate predator share two prey species, we find that stable coexistence of each species is possible over a range of parameters. When prey vigilance is either fixed or dynamic, stable coexistence is possible when α is small and β varies anywhere between zero and one (Fig. 2A). Similarly, when intermediate predator vigilance is either fixed or dynamic, stable coexistence is possible when c_N is small and β varies anywhere between zero and one (Fig. 2B). Thus, with alternative prey it is possible in both models for the top predator to attack the intermediate predator, but not to consume the intermediate predator, and for the system to still remain stable with all species persisting. In the model of two vigilant prey species, when vigilance is fixed at zero for both prey species, coexistence is not possible with the parameter values used in the example of Fig. 2A. When vigilance is fixed at relatively large values for both prey species, the system is stable over a larger range of α and β , but the system is no longer stable when $\beta = 0$. In the model of two prey species and vigilant intermediate predators, when vigilance is fixed at zero, the species can coexist, but over a smaller range of c_N values than when vigilance is either greater than zero or dynamic.

When vigilance is either dynamic or fixed at a relatively low value in both models (5) and (7), coexistence is possible at a low value of β because the top predator has its own prey resource that it is efficient at attacking. The intermediate predator must still have some advantage over the top predator that allows the top predator to attack the intermediate predator and not drive it extinct. Either the intermediate predator must utilize or attack the shared prey more efficiently, or the intermediate predator must have a lower mortality rate than the top predator. For the results in Fig. 2, we assumed that the intermediate predator had a lower mortality rate so that the attack rates on the prey species were symmetrical for both predator species. For the model with two vigilant prey species (model 5), we also assumed that the top predator encounter rate was higher with the prey species that had the less efficient ability to reduce predation through vigilance (i.e., lower g'_{R_i}). We made the same assumption for the intermediate predator species. This is a biologically reasonable assumption because a predator faced with a choice between two equally nutritious prey species will preferentially prey on the species that it has the greatest chance of killing (i.e., the

prey species with the lowest vigilance efficiency, g'_{R_i} ; Lima et al., 2003).

3.6. Influence of vigilance on top predator density with two prey resources

Given a low top predator consumption rate of the intermediate predator, how does the attack rate on the intermediate predator influence top predator density? We set $\beta = 0$ and followed the equilibrium density of the top predator over increasing values of α when the two prey resources were vigilant, and over increasing values of c_N when the intermediate predator was vigilant. As Fig. 3A shows, when prey vigilance was fixed, top predator density increased slightly with increasing α . Because vigilance was fixed, any increase in top predator density was due to decreasing competition with the intermediate predator. When both prey species were given optimal dynamic vigilance, however, top predator density again increased with α , but increased at a faster rate than when vigilance was fixed. This greater increase in density with dynamic prey vigilance occurred because increasing α values led to decreasing intermediate predator densities; decreases in intermediate predator density reduced competition, but also led to lower vigilance levels of the prey species preferred by the top predator (Fig. 3B). With lower optimal prey vigilance levels of its preferred prey, the top predator had higher equilibrium densities than when prey vigilance was fixed. As a consequence, even when the consumption rate of the intermediate predator is zero, higher attack rates on the intermediate predator by the top predator result in decreased competition and lower prey vigilance levels. These two factors combined lead to larger equilibrium densities of the top predator than does reduced competition alone.

We do not find this result if we assume that the intermediate predator is more efficient at consuming both prey species ($g_{R_1} > g'_{R_1}$ and $g_{R_2} > g'_{R_2}$). If this assumption is made, prey vigilance does not decrease with an increasing top predator attack rate on the intermediate predator. This result occurs because assuming the intermediate predator is a more efficient consumer of both prey species, the model becomes very similar to model (1), where we assumed the intermediate predator was a more efficient consumer of the single shared prey resource. We therefore expect the dynamics between the model of one prey resource and two prey resources to differ most when $g_{R_2} > g'_{R_2}$, and the top predator and intermediate predator are most efficient on different prey species. Thus, the results of Fig. 3A and B require partitioning of prey resources by the top and intermediate predators.

When the intermediate predator is vigilant and $\beta = 0$, top predator equilibrium density increases faster when the intermediate predator is not vigilant, than when the intermediate predator has dynamic vigilance (Fig. 3C). Top predator density increases faster when there is no vigilance in this example because increasing c_N results in directly reducing competition with the intermediate predators through the death of intermediate predators. When the intermediate predators have dynamic vigilance,

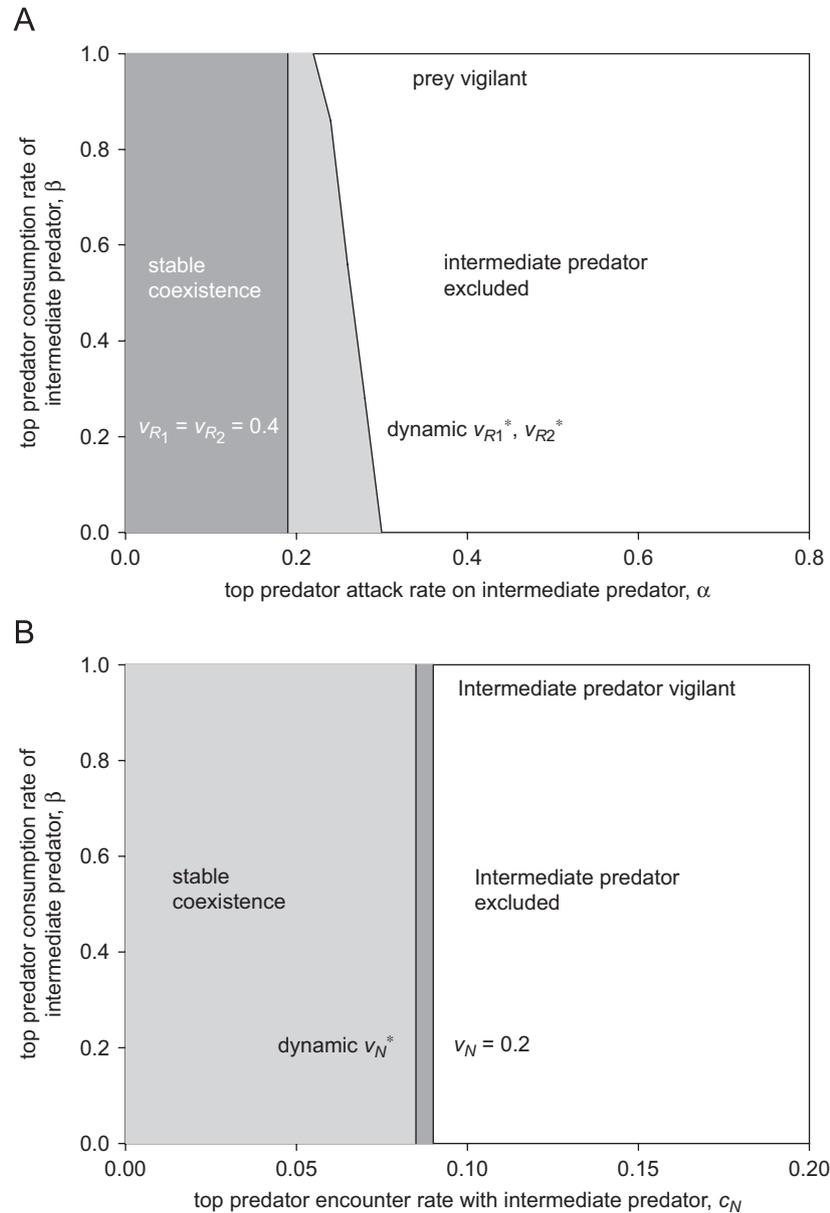


Fig. 2. Regions of locally stable coexistence when the top predator and intermediate predator share two prey resources. In the regions where stable coexistence does not occur, the intermediate predator is excluded: (A) the prey is vigilant. Coexistence is plotted over a range of top predator attack rates on, and top predator consumption rates of, the intermediate predator. The regions of coexistence are for dynamic optimal vigilance by both prey species (v_{R1}^*, v_{R2}^*), and fixed vigilance $v_{R1} = v_{R2} = 0.4$. The region of coexistence for a given vigilance begins at its solid line, and extends to all α and β values to the left of the line. Parameters are $r_1 = r_2 = 1$, $K_1 = K_2 = 1$, $b_1 = b_2 = b'_1 = b'_2 = 1$, $m = 0.1$, $m' = 0.17$, $c_{R1} = c'_{R2} = 1$, $c_{R2} = c'_{R1} = 0.1$, $l_{R1} = l_{R2} = l'_{R1} = l'_{R2} = 1$, $g_{R1} = g'_{R2} = 10$, and $g_{R2} = g'_{R1} = 50$. (B) The intermediate predator is vigilant. Coexistence is plotted over a range of top predator encounter rates with, and top predator consumption of, the intermediate predator. The regions of coexistence are for dynamic optimal vigilance (v_N^*), and fixed vigilance $v_N = 0.2$. The region of coexistence for a given vigilance begins at its solid line, and extends to all c_N and β values to the left of the line. Parameters are $m' = 0.15$, $l_N = 1$, $g_N = 10$, $a_1 = a'_2 = 0.167$, $a_2 = a'_1 = 0.02$. All of the other parameter values as in (A).

however, competition is reduced indirectly by increases in vigilance, resulting in a comparatively lower top predator equilibrium density. The top predator density plateaus in this example when the intermediate predator is not vigilant, because the intermediate predator goes extinct at high values of c_N . Intermediate predators do not go extinct at these values of c_N when they are dynamically vigilant, showing how intermediate predator vigilance increases the range of parameters over which the system is stable.

Fig. 3D illustrates how the optimal intermediate predator vigilance increases quickly with c_N , helping to stabilize the system.

3.7. Stabilizing influence of vigilance with two prey resources

We examined the stabilizing influence of vigilance by first considering systems with either fixed prey or

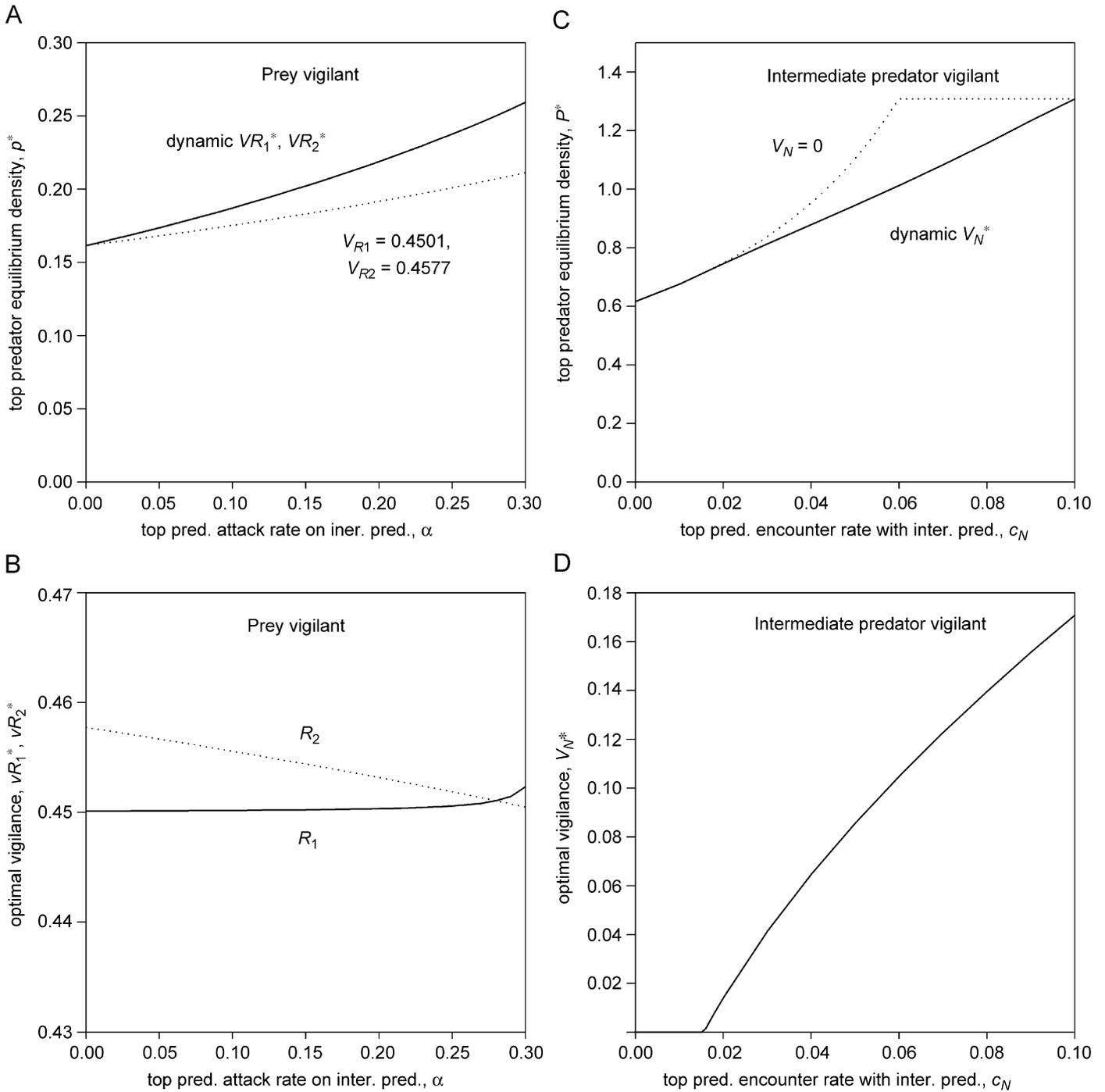


Fig. 3. (A) Top predator equilibrium density over a range of attack rates on the intermediate predator, with no consumption of the intermediate predator ($\beta = 0$), and with vigilant prey. The dotted line is the top predator density with fixed prey vigilance ($v_{R1} = 0.4501, v_{R2} = 0.4577$), where the increase in top predator density with increasing α is due to decreasing competition with the intermediate predator. The solid line is the top predator density with dynamic optimal vigilance by both prey species, where the increase in top predator density with increasing α is due to decreases in both competition and prey vigilance. (B) Optimal vigilance levels of both prey species for the same model as in (A). The solid line is the vigilance level of prey species 1, and the dotted line is the vigilance level of prey species 2 (the prey ‘preferred’ by the top predator). (C) Top predator equilibrium density over a range of encounter rates with the intermediate predator, with no consumption of the intermediate predator ($\beta = 0$), but vigilant intermediate predators. The dotted line is the top predator density with fixed intermediate predator vigilance ($v_N = 0$). The solid line is the top predator density with dynamic optimal vigilance by the intermediate predator. (D) Optimal vigilance level of the intermediate predator for the same model as in (C). All other parameter values as in Fig. 2.

intermediate predator vigilance, and then the same systems with dynamic vigilance, allowing systems to go to equilibrium, and then perturbing the density of one of the species in the system. We found that the systems with

dynamic optimal vigilance returned to equilibrium with smaller amplitude cycles than did the systems with fixed vigilance. Fig. 4A show a typical time-series for a system with prey vigilance and $\beta = 0$ after perturbing the density

of the intermediate predator from equilibrium. Intermediate predator density returned to its equilibrium density faster when the prey species had dynamic vigilance than when they had fixed vigilance. Fig. 4B shows a similar time-series, but with intermediate predator vigilance, $\beta = 0$, and perturbation of the top predator density. Again, intermediate predator density returns to its equilibrium faster when the intermediate predator has dynamic vigilance than when it has fixed vigilance. Dynamic vigilance in a system

with IGP can thus help to stabilize the system, in the sense of helping to dampen perturbations from equilibrium.

4. Discussion

This paper began by asking how a system with intraguild predation (IGP) could be stable if the top predator did not gain significantly from consumption of the intermediate predator. If the top and intermediate

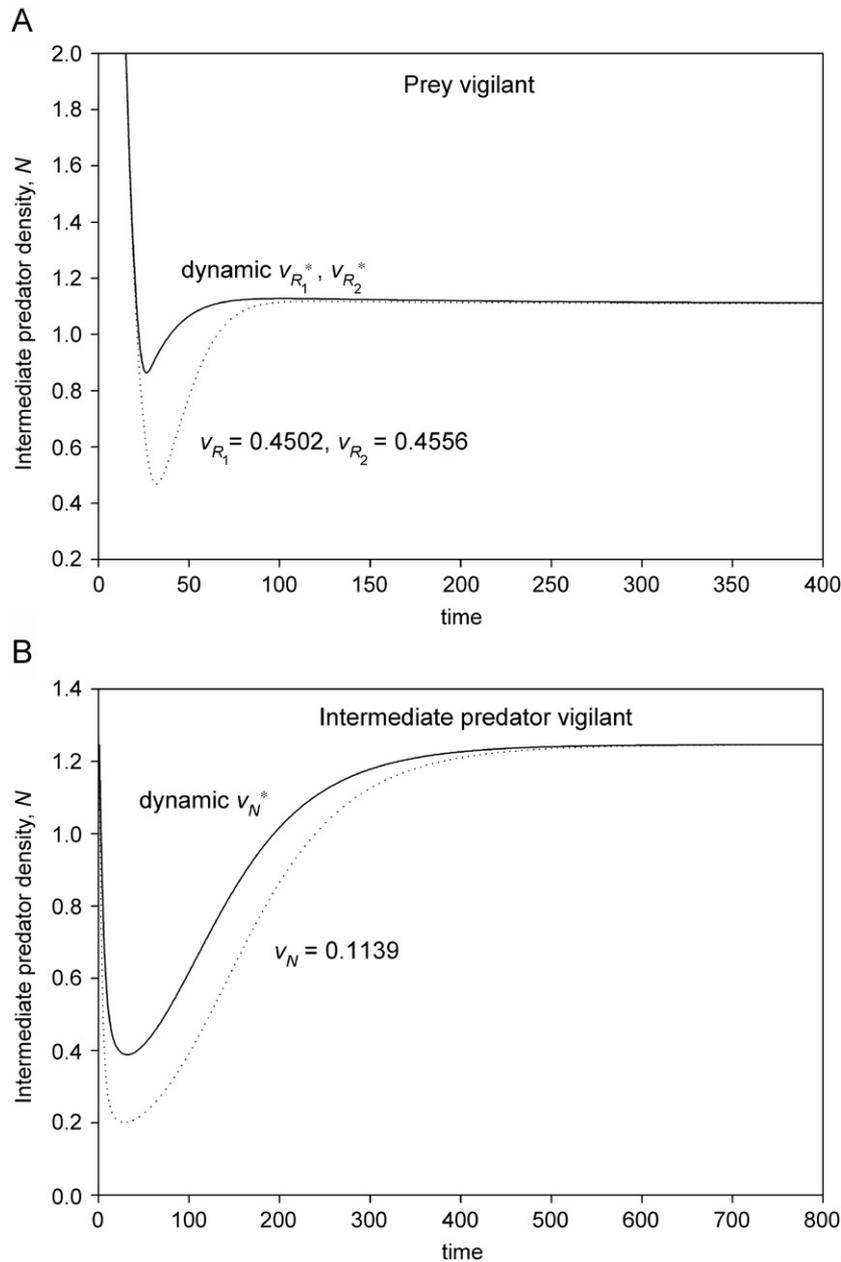


Fig. 4. Time-series of intermediate predator density after perturbation. The solid line in each panel is the time-series for systems with dynamic vigilance, and the dotted lines are for systems with fixed vigilance. The systems were at equilibrium at time zero, and were then perturbed: (A) prey are vigilant, and at time zero the intermediate predator density was perturbed to 9.0. The equilibrium values at time zero for each species were $R_1^* = 0.6317$, $R_2^* = 0.9295$, $N^* = 1.1099$, and $P^* = 0.1872$. The fixed prey vigilance levels were set to the equilibrium vigilance levels of the dynamic system ($v_{R_1}^* = 0.4502$, and $v_{R_2}^* = 0.4556$.) $\alpha = 0.1$. (B) Intermediate predators are vigilant, and at time zero the top predator density was perturbed to 9.0. The equilibrium values at time zero for each species were $R_1^* = 0.8537$, $R_2^* = 0.6937$, $N^* = 0.4633$, and $P^* = 1.723$. The fixed intermediate predator vigilance level was $v_N^* = 0.1139$. $c_N = 0.065$. In both panels, $\beta = 0$, and all other parameter values as in Fig. 2.

predators share only one prey species, the top predator must indeed consume the intermediate predator, at least a little, for stable coexistence to occur. There is a relationship between the top predator consumption rate of the intermediate predator and the top predator attack rate on the intermediate predator, though, such that the system can be stable if the top predator rarely consumes the intermediate predator but has a high attack rate on the intermediate predator. Vigilance by the prey or the intermediate predator can increase the region of coexistence, given these assumptions.

As the models with two prey resources show, however, systems with IGP can be stable even if the top predator never consumes the intermediate predator. This can occur if the top predator and intermediate predator share more than one prey species. As a result, we would expect mammalian top predators that attack but do not consume an intermediate predator to consume at least two different prey resources. Holt and Polis (1997) suggest that alternative prey can help stabilize IGP, and these results match that expectation. Holt and Huxel (in press), though, show that alternative prey can also at times be destabilizing in IGP.

By sharing two prey species, the top predator can survive without consuming the intermediate predator, so why does the top predator still go to the trouble of attacking the intermediate predator? In model (7), when there are two prey species and the intermediate predator is vigilant, attacking the intermediate predator allows the top predator to indirectly reduce competition for the shared prey. In model (5), when the prey are vigilant, attacking the intermediate predator not only reduces competition with the top predator, it also reduces the vigilance of the top predator's preferred prey. Thus, even though we assumed the intermediate predator was relatively inefficient at attacking the top predator's preferred prey, attacking the intermediate predator and thereby reducing its density led to less vigilance by the top predator's preferred prey, and subsequently a higher equilibrium density for the top predator.

Vigilance may not only allow the top predator to persist over a broader range of consumption rates of the

intermediate predator, under certain conditions it may also help to stabilize the system. We found that in systems where prey or intermediate predators are dynamically vigilant, the ability of vigilance levels to change adaptively to changes in other species' densities resulted in dampening of population cycles after perturbations in a species' density. Previous one prey–one predator and two prey–one predator models have suggested that adaptive prey responses to predation can increase the stability, or decrease the population fluctuations, of the system (Brown et al., 1999; Fryxell and Lundberg, 1998; Kimbrell and Holt, 2004; Křivan, 1998). We extend these results to IGP, and further extend them by allowing the intermediate predator, and not just the basal prey, to respond behaviorally. We find that in systems with IGP that are perturbed, prey and intermediate predator vigilance may be a stabilizing force that helps systems to persist. In the models and parameter choices examined in this paper, even with fixed vigilance the systems tend to be relatively stable. However, systems with IGP can be strongly unstable despite mutual invasibility with either one (Holt and Polis, 1997), or multiple (Holt and Huxel, in press) prey species. A challenge for future work is to examine the effect of dynamic vigilance when the intrinsic dynamics are unstable. The main results of this paper are summarized in Table 1.

Our models of prey vigilance assumed that predator and prey births were continuous through time, and that prey vigilance had an immediate influence on both predator and prey births. If we assume, however, that prey vigilance changes much more rapidly than do changes in predator and prey births, then the dynamical consequences of top predators attacking intermediate predators may be enhanced. As shown in Appendix C, when top predator and prey densities are held constant, decreases in intermediate predator density lead to large decreases in optimal prey vigilance. We saw increasing prey vigilance with increasing top predator attack rates on the intermediate predator in the model of one shared prey resource (model 1) because the reduced intermediate predator density led to immediate increases in prey density. However, if prey births are seasonal or occur after a lag, modest decreases in

Table 1
Summary of main results for each of the four models

	Can system persist when top predator never consumes inter. predator?	Does increasing top predator attack/encounter rate with inter. predator cause prey/inter. predator vigilance to increase or decrease?	Can vigilance help the system to persist?
One prey, prey vigilant	No	Increase	Yes
One prey, inter. predator vigilant	No	Increase	Yes
Two prey, prey vigilant	Yes	Decrease	Yes
Two prey, inter. predator vigilant	Yes	Increase	Yes

intermediate predator density due to attacks by the top predator may (at least temporarily) lead to relatively large decreases in optimal prey vigilance. This may further help explain why top predators attack intermediate predators that they do not consume.

Spatial dynamics may play a similar role when the intermediate predator is vigilant (Brown, 1999). If the intermediate predator becomes very vigilant when entering a patch that contains a top predator, this may greatly increase the ability of the top predator to compete with the intermediate predator for shared prey. This also suggests a possible reason for *why* the top predator might not consume the intermediate predators it has killed. The top predator may kill the intermediate predator and leave it unconsumed as a signal to other intermediate predators that there is a top predator in that patch. The models examined in this paper were not spatially explicit, but we can use the model of two prey resources and vigilant intermediate predators (model 7) to suggest the dynamical results of a top predator leaving intermediate predators unconsumed as a means of increasing intermediate predator vigilance.

As Fig. 5 shows, at low top predator encounter rates with the intermediate predator, when the top predator kills but does not consume the intermediate predator and thereby induces a high vigilance level in the remaining intermediate predators ($v_N = 0.35$, $\beta = 0$), the top predator has a relatively high equilibrium density. This top predator density is in fact greater than when the top predator consumes the intermediate predator, thereby not inducing any vigilance in the remaining intermediate predators ($v_N = 0$, $\beta = 1$). We suggest that spatial dynamics may be

necessary for this effect to be maintained adaptively because the vigilance level that would need to be induced in the intermediate predator is higher than the optimal vigilance level in a mean-field model (at low values of c_N , the optimal vigilance level in model (7) is zero). It may be optimal, however, for an intermediate predator entering a patch that it knows to contain a top predator to have a very high vigilance level. At higher c_N values this effect is reversed, suggesting that consuming the intermediate predator leads to a higher top predator density. Future studies should examine the role that spatial dynamics play in modulating the evolution and ecological impact of intermediate predator vigilance.

This paper was inspired by mammalian carnivore systems with IGP—specifically, the surprisingly high frequency with which top mammalian carnivores kill but do not consume intermediate carnivores (Palomares and Caro, 1999). It would be interesting to know if the frequency of top predators that attack but do not consume intermediate predators is similar in other vertebrate and invertebrate systems. The high observed frequency of mammalian top predators that do not consume intermediate predators may result from the fact that it is relatively easier to observe large mammals and their interactions with intraguild members, than to observe interactions among smaller vertebrate or invertebrate species. It may be possible that the role of vigilance in mammalian systems is comparable to that played by other modalities of phenotypic or behavioral plasticity in other systems. If so, the results in this paper, with some modifications, may prove to be applicable to a wide range of ecological systems.

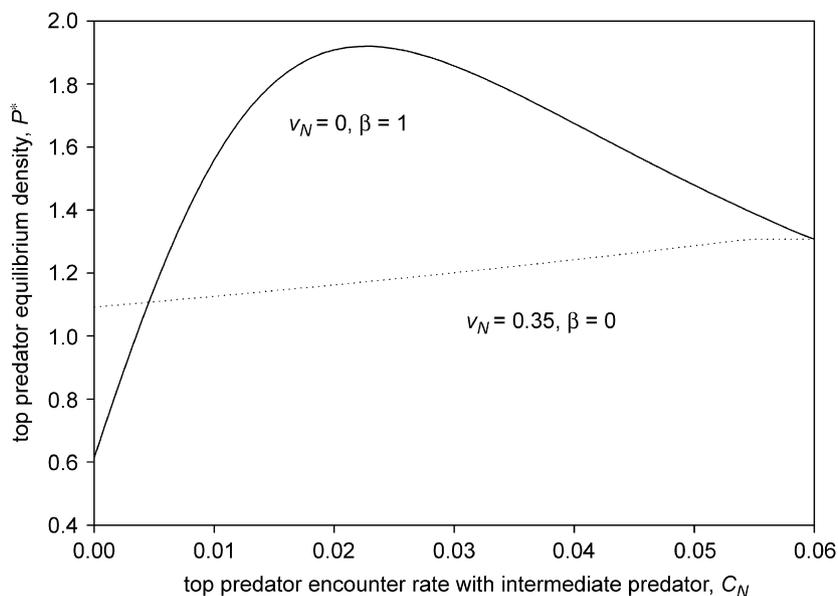


Fig. 5. Top predator equilibrium densities over a range of encounter rates with the intermediate predator, with vigilant intermediate predators and two shared prey. The solid line shows intermediate predators without vigilance, and top predators always consuming the intermediate predators they kill ($v_N = 0$, $\beta = 1$). The dotted line shows intermediate predators with fixed vigilance, and top predators never consuming the intermediate predators they kill ($v_N = 0.35$, $\beta = 0$). All other parameters values as in Fig. 2.

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Appendix A

In this appendix we graphically explore how the ability of prey vigilance to reduce predation by the intermediate and top predators (g_R and g'_R , respectively) influences the coexistence of the system with one prey species. We also explore how prey carrying capacity, K , influences the coexistence of the system with one prey species when prey or intermediate predators are vigilant.

Fig. A1 shows the regions of coexistence for different values of g_R and g'_R for the model of one prey resource and fixed prey vigilance (model 1). Coexistence occurred over a relatively large range of parameter values when the fixed vigilance was at a relatively low level; a higher level of vigilance resulted in a smaller region of coexistence. When prey had dynamic vigilance, the region of coexistence was similar to the region when prey had a relatively high fixed vigilance (similar to the region of coexistence when $v_R = 0.7$ in Fig. A1). Regions of coexistence only occur when $g'_R > g_R$. When $g'_R < g_R$, the top predator excludes the intermediate predator from the system. At large g_R values, the system is not stable even when $g'_R > g_R$. The reason is that at large g_R values, the intermediate predator has such a low attack rate on the prey that the intermediate predator density is too low to sustain the top predator, and the top predator goes extinct.

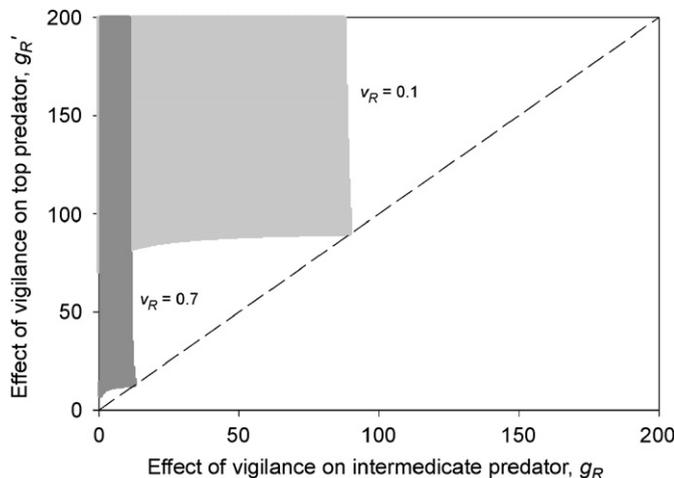


Fig. A1. Regions of coexistence for the model of one prey resource with fixed vigilance over several values of g_R and g'_R . The light gray region is for $v_R = 0.1$, and the dark gray region is for $v_R = 0.7$. The dashed line is the 1:1 line. The parameters are $r = 1$, $K = 1$, $b = b' = 1$, $m = m' = 0.1$, $c_R = c'_R = 1$, $l_R = l'_R = 1$, and $\alpha = \beta = 0.5$. Similar figures arise for other parameter choices.

We next examine how prey carrying capacity influences the stability of the system. Intraguild predation theory predicts that as resource productivity increases, top predators will increase in density, and will drive the intermediate predator extinct at high resource productivities (Holt and Polis, 1997). However, empirical studies have observed systems with high resource productivities with apparently stable coexistence of both predators and prey (e.g. Borer et al., 2003). Křivan (2000) and Křivan and Diehl (2005) used theoretical models to show that adaptive foraging by a top predator could lead to stable coexistence of a system with intraguild predation at high resource productivities.

The influence of productivity on coexistence of a system with intraguild predation could also be influenced by vigilance. To examine the effect of vigilance and resource productivity on coexistence, we characterized the regions of

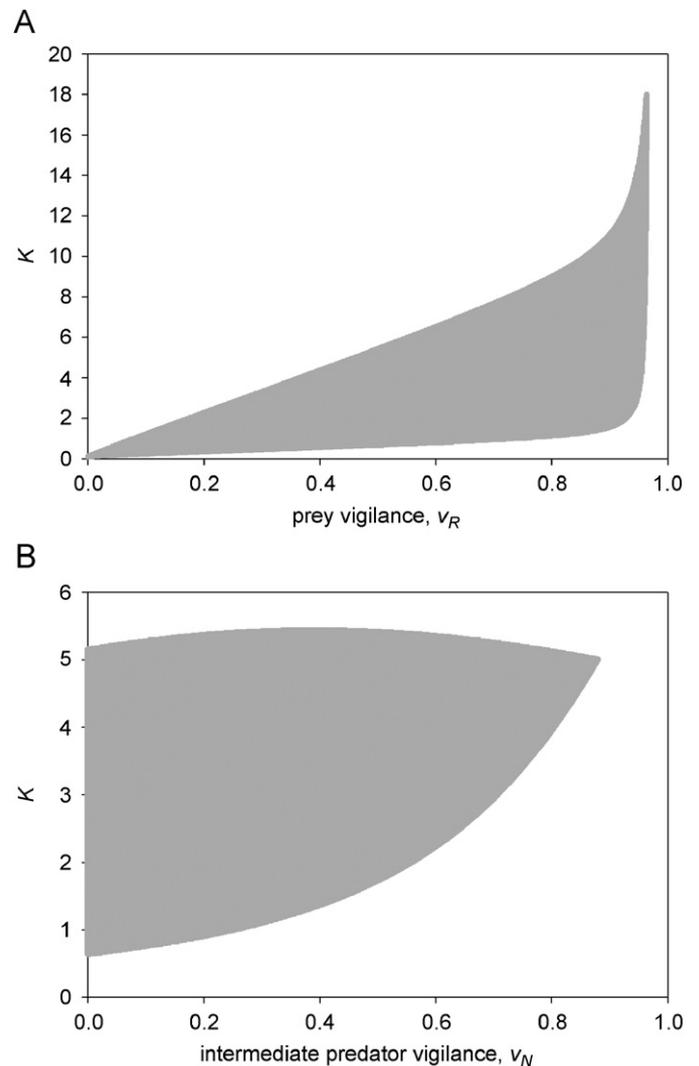


Fig. A2. Regions of coexistence over different levels of vigilance and prey carrying capacity, K , for (A) a single prey resource and vigilant prey, and (B) a single prey resource and vigilant intermediate predators. In (A) $g_R = 10$, $g'_R = 100$, and all other parameters as in Fig. A1. In (B) $l_N = 1$, $g_N = 10$, $c_N = 1$, $a = 0.167$, $a' = 0.02$, and all other parameters as in Fig. A1.

coexistence of the model with one shared prey and fixed prey or intermediate predator vigilance over a range of vigilance levels and prey carrying capacities, K (we consider K to represent resource productivity in the model). Similar to previous studies (Holt and Polis, 1997), we found that when K was very low, and either the prey or the intermediate predator was vigilant, the top predator went extinct. When K was high, the intermediate predator was driven to extinction. However, when prey were vigilant, the range of K values over which the system was stable increased with vigilance level (Fig. A2A). Furthermore, the system was stable at high K values when prey vigilance levels were also high.

When prey had dynamic vigilance, the optimal level of vigilance was determined by the carrying capacity of the prey. As the carrying capacity increased, the optimal vigilance of the prey also increased, but remained at an intermediate level ($v_R^* \sim 0.45$) over the range of carrying capacities that the system was stable. The range of carrying capacities over which the system with dynamic prey

vigilance was stable was bounded by the range over which the system was stable when prey had fixed vigilance (Fig. A2).

When intermediate predators had fixed vigilant (Fig. A2B), as intermediate predator vigilance increased, the range of K values that led to stable coexistence became smaller. Interestingly, the highest K value that led to coexistence occurred at an intermediate level of predator vigilance. When intermediate predators had dynamic vigilance, the optimal level of vigilance increased with prey carrying capacity. The optimal level of vigilance was near zero at low carrying capacities, and then increased to an intermediate level at higher carrying capacities. However, the range of carrying capacities over which the system was stable was bounded by the region of coexistence when intermediate predators had fixed vigilance.

Consequently, when either the prey or the intermediate predator is vigilant, vigilance can have a large influence on the range of resource productivities over which a system with intraguild predation is stable.

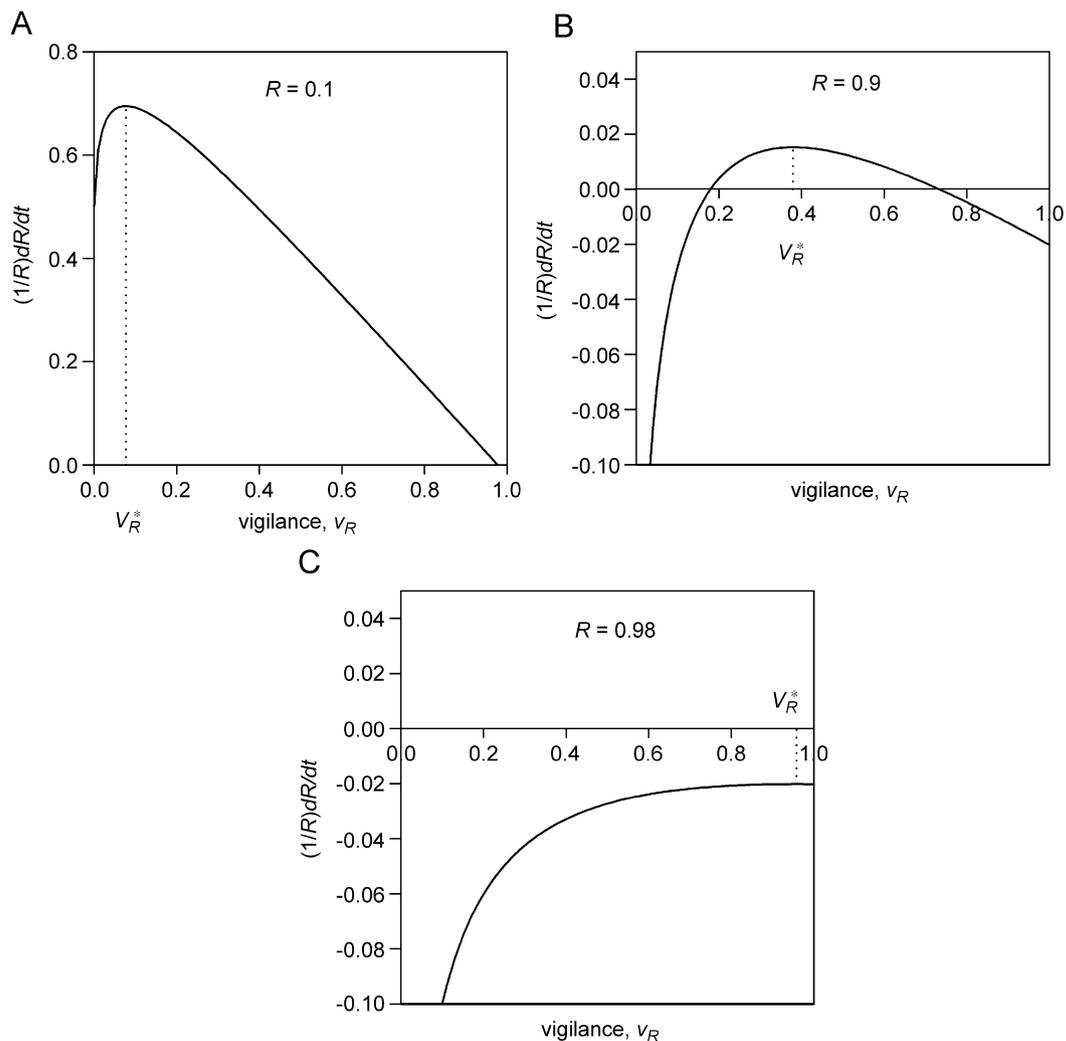


Fig. B1. Per capita prey growth rate as a function of vigilance when (A) $R = 0.1$, (B) $R = 0.9$, and (C) $R = 0.98$. The dashed line indicates the highest per capita prey growth rate over the range of vigilance levels, and is therefore the optimal vigilance level (v_R^*) for that prey density. The other parameters are $r = 1$, $K = 1$, $c_R = c'_R = 1$, $l_R = l'_R = 1$, $g_R = 10$, $g'_R = 100$, $N = P = 0.2$.

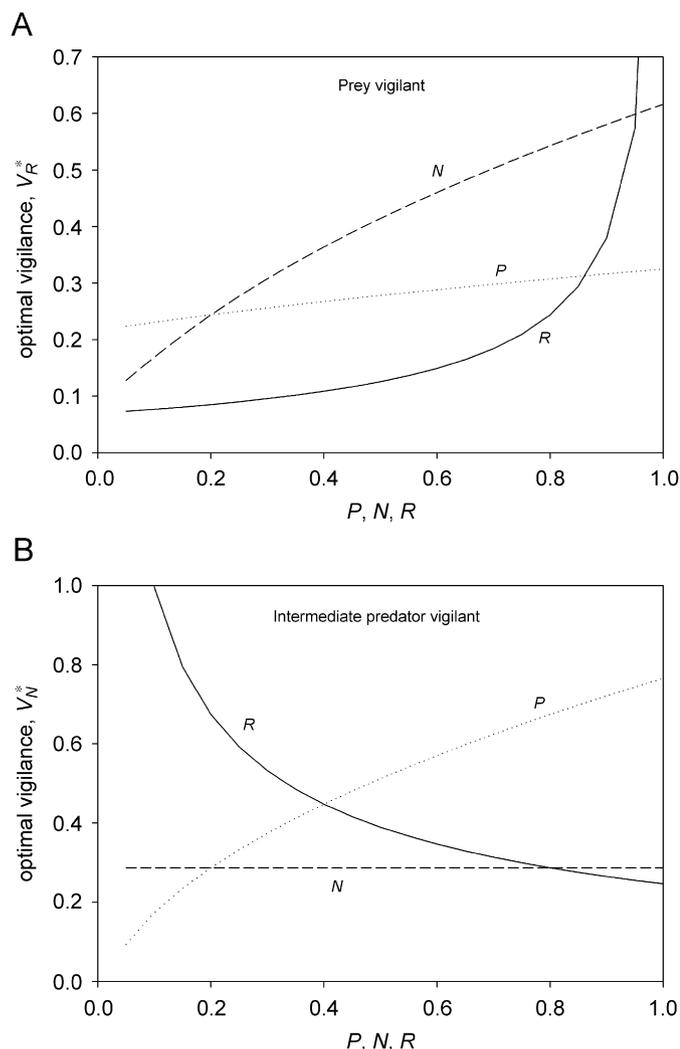


Fig. C1. Optimal vigilance levels over a range of top predator, intermediate predator, and prey densities: (A) prey are vigilant and (B) intermediate predators are vigilant. In both panels, the dotted line is the change in optimal vigilance levels over a range of P densities, while N and R are held constant. The dashed line is the change in optimal vigilance over a range of N densities, while the other species are held constant. The solid line is the change in optimal vigilance over a range of R densities, while the other species are held constant. When they are held constant, we set $P = 0.2$, $N = 0.2$, $R = 0.8$, and all other parameter values as in Fig. 1. Similar patterns emerge for other choices of fixed P , N , and R .

Appendix B

To find the optimal vigilance level for the prey we determine the vigilance level that returns the highest per capita growth rate for the prey. The per capita prey growth rate $((1/R)(dR/dt))$ can be thought of as a fitness function for an individual of the prey species. Fig. B1 shows the per capita prey growth rate for the model with one shared prey resource over a range of prey vigilance levels for several fixed values of prey density, R , and with fixed values of N and P . When prey density is low (Fig. B1A), the per capita prey growth rate is positive over almost the entire range of vigilance levels, but is highest at

a relatively low level of vigilance ($v_R^* = 0.077$). As R increases (Fig. B1B and C), the per capita prey growth rate is lower, and may in fact be negative over the entire range of vigilance levels (Fig. B1C). Nonetheless, we can still find the vigilance level that returns the highest per capita prey growth rate. In practice, we determined the optimal vigilance level by differentiating the per capita prey growth rate with respect to v_R , setting the resulting equation equal to zero, and then solving for v_R . Interestingly, as prey density increases, the per capita prey growth rate as a function of vigilance flattens, meaning that increases in vigilance becomes less costly. As mentioned in the text, this is one of the reasons that the optimal prey vigilance level increases with increasing prey density. When the intermediate predator was vigilant, we found the optimal vigilance in a similar way using the intermediate predator per capita growth rate.

Appendix C

In this appendix we explore how the density of the predator species and the density of the prey in the model with one prey resource affect the optimal level of prey or intermediate predator vigilance. Fig. C1A and B shows how optimal prey and intermediate predator vigilance levels shift as densities of the top predator, intermediate predator, and prey are changed one at a time, while the other two densities are held constant. Optimal prey vigilance increases faster with intermediate predator density than with top predator density, because we have assumed the intermediate predator to be a more efficient predator on the prey. Optimal prey vigilance also increases with prey density—the reasons for this are discussed in the main text. Optimal intermediate predator vigilance increases with increasing predator density, but decreases with increasing prey density. (The density of the intermediate predator does not influence the level of its own vigilance, because we did not include direct density dependence of the intermediate predator on itself.)

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