Evolutionary Ecology Research, 2010, **12**: 307–325

The impact of adaptive defence on top-down and bottom-up effects in systems with intraguild predation

Peter A. Abrams and Simon R. Fung

Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada

ABSTRACT

Questions: How does adaptive prey defence alter the responses of a system with intraguild predation to the bottom-up effects of enrichment and the top-down effects of predator mortality? Is the cost of defence an important determinant of the answer to this first question? Is persistence and/or increase of the prey population following enrichment more likely when the prey have adaptive defence?

Methods: General equilibrium analysis of a simple model of the three-species intraguild predation system is used to determine the signs of population responses to top-down and bottom-up perturbations. Simulations are used to explore systems with unstable dynamics.

Key assumptions: The system consists of three species, and all consumer species have linear functional responses in the absence of flexible prey defence.

Results: Adaptive defence allows the equilibrium prey abundance to increase with enrichment of the basal resource. Defence may allow prey persistence over all possible levels of enrichment when high levels of defence imply near-immunity from predation. Predicting the direction of change in prey abundance in response to top-down or bottom-up perturbations requires knowledge of the costs of prey defence. The direction of response of abundance to a perturbation often changes sign when the perturbation shifts the system from stable to cyclic dynamics. Given costly defence, intraguild predation systems and food chains exhibit qualitatively similar responses to top-down and bottom-up perturbations in stable systems.

Keywords: adaptive behaviour, anti-predator behaviour, bottom-up effect, food chain, intraguild predation, omnivory, top-down effect.

INTRODUCTION

In their seminal theoretical work on intraguild predation (IGP), Holt and Polis (1997, p. 745) pointed out that: 'Persistent strong IGP raises a puzzle of species coexistence, particularly in productive environments'. This was based on their finding that exclusion of the prey

Correspondence: P.A. Abrams, Department of Ecology and Evolutionary Biology, University of Toronto, 25 Harbord Street, Toronto, Ontario M5S 3G5, Canada. e-mail: peter.abrams@utoronto.ca

occurred at high prey carrying capacities in a Lotka-Volterra type model with three species (a predator, a prey, and a resource, with the predator feeding on the resource as well as the prey). The contradiction between the observation of extensive intraguild predation in productive environments and the exclusion predicted by the Holt-Polis model continues to generate new theoretical analyses (e.g. Amarasekare, 2008). A variety of more detailed models have supported the finding of likely prey exclusion in sufficiently productive environments (Mylius *et al.*, 2001; Kooi *et al.*, 2002; Kuijper *et al.*, 2003; van de Wolfshaar *et al.*, 2006). Exceptions to this pattern due to direct self-limitation of the predator and refuges of the prey have also been noted (Gismervik and Anderson, 1997; Křivan, 2000; Hart, 2002; Amarasekare, 2007a, 2007b, 2008). Nevertheless, the observation of intraguild predation in productive environments continues to be regarded as puzzling (Arim and Marquet, 2004; Křivan and Diehl, 2005; Rosenheim, 2007; Amarasekare, 2008).

Holt and Polis's (1997) original discussion included the suggestion that adaptive anti-predator behaviour by the prey species was one of several factors that might allow persistence. However, they did not present any formal analysis of this case. In the intervening 12 years, this suggestion has received relatively little attention, in spite of rapid growth in studies of adaptive anti-predator behaviour in linear food chains (for reviews, see Bolker *et al.*, 2003; Abrams, 2010) and continued interest in intraguild predation (e.g. Rosenheim, 2007, and associated Special Feature articles). There is some empirical evidence that predator avoidance mechanisms account for the presence of some prey species rather than others in the presence of intraguild predators (e.g. Moehrenschlager *et al.*, 2007).

Prey exclusion with greater enrichment is one way in which IGP systems have been argued to differ from food chains lacking intraguild predation. In addition, Polis and Strong (1996) argued that intraguild predation might eliminate the expected positive impact of increased predator abundance on resource abundance (i.e. trophic cascade) expected in simple food chains. However, there has apparently been no analysis of the nature of top-down impacts in IGP systems using simple models with general functional forms. In this article, we explore the effects of adaptive prey defence on the responses of species abundances to both enrichment and increased mortality (e.g. harvest) of the top predator in the context of the three-species IGP food web studied by Holt and Polis (1997). These results will be used to revisit the question of whether IGP systems are likely to respond to environmental change in a fundamentally different manner than do food chains.

The logic underlying the suggestion that anti-predator behaviour could influence the persistence of prey in IGP systems is the idea that flexible defence should allow prey to reduce their risk from predation when predators become common. However, because defence generally entails costs (Lima and Dill, 1990; Werner and Peacor, 2003), it is not clear that the balance of benefits and costs will be sufficient to prevent prey exclusion in productive environments. In addition, it has long been known that adaptive defence can alter the stability and dynamics of predator–prey systems in ways that could affect persistence (Abrams, 1984, 1992; Abrams and Matsuda, 1997). Several models of food chains (Abrams, 1992, 1995; Abrams and Vos, 2003) have shown that defence can reverse the normal directions of change in abundance entailed by top-down and bottom-up effects. For example, increased predator abundance can increase prey abundance, by causing prey to reduce over-exploitation of their own food. Peacor (2002) obtained experimental evidence for such an effect in a food chain system with larval amphibians as prey. This raises the question of whether similar effects might also occur in IGP systems, and whether these might affect Polis and Strong's (1996) speculation that intraguild predation prevents trophic cascades.

We know of only one analysis of a model with a general type of adaptive defence in an IGP system (Kimbrell *et al.*, 2007). Amarasekare (2006, 2007b), however, has carried out some modelling of IGP systems in a metapopulation context, which has included scenarios when prey movement is related to fitness. These previous works are treated in more detail in the Discussion. Our analysis here examines a wide range of types of anti-predator behaviour and broader classes of functional relationships between defence and other fitness components. To simplify the analysis, we assume that only the prey species (not the resource) exhibits flexible anti-predator behaviour. The interaction of two behavioural variables in a food web can lead to many unexpected consequences (Abrams, 1992), and the case of interacting defences in prey and resource species will be considered elsewhere.

MODELS AND ANALYSIS

To determine the impacts of adaptive balancing of the costs and benefits of prey defence, we begin our analysis by examining cost-free defence. It has been known for some time (Abrams, 1982, 1984) that anti-predator behaviour by a prey species produces predator-dependent functional responses, i.e. the intake rate of prey by an average predator declines with predator density (Abrams, 1984, 1994; Fryxell and Lundberg, 1998; Brown *et al.*, 1999). The simplest type of model of defence assumes that the capture rate of prey per unit time by a searching predator is a decreasing function of predator density. The predator-dependent Beddington-DeAngelis functional response (DeAngelis *et al.*, 1975) is a specific way of representing such an effect. The predator dependence is a consequence of the prey reducing their exposure when predators are more abundant. Because this does not reflect any cost of anti-predator behaviour, it is most appropriate when such costs are small. Some numerical work has shown that prey densities can increase with enrichment of IGP systems that have predator-dependent functional responses (Hart, 2002). The first model explored here generalizes these numerical results to show how the nature of predator dependence in the functional response is likely to affect the responses of the population densities of all three species to increased resource productivity or predator mortality.

This section is followed by an analysis of a family of models in which a cost of anti-predator behaviour is present, and the level of defence is based on a behaviour that changes in a manner that increases current individual fitness (Abrams *et al.*, 1993). Different types of cost are considered, and the ability of the prey to persist at high productivities as well as the response of prey abundance to top-down and bottom-up impacts are analysed. Most of the models assume linear functional responses of the consumers, given a fixed prey behaviour. This assumption is particularly likely to lead to prey exclusion, because there is no limit to how much the predator can consume. Thus, we examine the impact of defence in those cases where prey persistence in high productivity environments is least likely.

Systems with predator-dependent functional responses (no cost of defence)

A number of mechanisms other than prey defence can produce predator-dependent functional responses (Abrams, 1994; Abrams and Ginzburg, 2000). These include a limited number of high-quality hunting locations and aggressive interactions between predators. Experimental results support the widespread presence of predator dependence in functional responses (Skalski and Gilliam, 2001), although the mechanism is usually not known. The models used here assume that greater predator abundance reduces the predators' per capita capture rate of

prey, but has no effect on any other fitness-related parameter of the prey. The attack rate parameter of predator on prey in a non-predator-dependent response is replaced by a decreasing function of P that is bounded below by zero. Thus, instead of a constant per capita attack rate of predators on prey, denoted S_2, this attack rate is multiplied by a factor f, where $0 < f < 1$, and f is a decreasing function of predator density, P. The functional and numerical responses are linear functions of food density, as in the model of Holt and Polis (1997). This scenario is described by:

$$\frac{dR}{dt} = R(r - k(R) - CN - S_1P)$$

$$\frac{dN}{dt} = N(BCR - D - S_2Pf(P)) \qquad \text{(1a, b, c)}$$

$$\frac{dP}{dt} = P(e_1S_1R + e_2S_2f(P)N - d)$$

where S_2 is now the maximum per capita attack rate. The maximum per capita growth rate of the resource is r, which is decreased by $k(R)$, a non-negative increasing function reflecting density dependence in resource growth. In the simplest case of logistic growth $k(R) = rR/K$, where K is the carrying capacity in the normal parameterization of the logistic. Enrichment could increase r, and could also decrease k (e.g. by increasing K if the function is logistic). The parameters D and d are per capita death rates; B, e_1, and e_2 are conversion efficiencies; and C, S_1, and S_2 are maximum per capita capture rates. The total instantaneous capture rate of prey by predators is S_2fPN; this rate decreases with increasing predator abundance if $f + f'P < 0$, and increases if this inequality is reversed. (The prime denotes the derivative of the function; $f' = df/dP$.) The quantity $f + f'P$ determines the sign of the derivative of the prey's per capita risk of predation with respect to predator density. It is common to assume that this quantity increases with the number of predator individuals, but optimization models based on flexible defence (Abrams, 1993) show that this need not be true. A commonly used form in models with predator-dependent responses is $f = 1/(1 + \alpha P^m)$, where α and m are positive constants. This function produces a decrease in risk to a prey individual with increasing predator abundance at large P when $m > 1$.

There are several ways to model greater per capita growth of the resource in the context of this model. The most direct approach is to increase r, which increases both the maximum per capita growth rate and the equilibrium density of the resource. A model of density-dependent resource growth may be derived from a more detailed model in which the resource species consumes an abiotic nutrient that has chemostat nutrient growth and a type-2 resource functional response (Abrams, 2009). In this case, the maximum per capita growth rate (r) reaches an asymptote with increased nutrient input, while the equilibrium density grows linearly with input rate (Abrams, 2009). If the resource has a linear functional response, both its maximum per capita growth rate and carrying capacity increase linearly with input. The approach taken here will be to examine the impacts of increasing r in the context of the general model of resource growth in equations (1), and the impact of increasing K in the context of a logistic model.

The impact of an increased resource r on the three equilibrium population densities may be determined by implicit differentiation of the conditions for an equilibrium of equations (1) at which all population densities are positive. The resulting expressions are:

$$\frac{\partial P}{\partial r} = e_2 BCf/Q$$

$$\frac{\partial N}{\partial r} = \left(-e_2 BCNf' - e_1 S_1 (f + Pf')\right)/Q \qquad \text{(2a, b, c)}$$

$$\frac{\partial R}{\partial r} = e_2 f(f + f'P)/Q$$

where $Q = -(BCe_2 N + e_1 S_1 P)Cf' + e_2 S_2 f^2 k' + (CS_1(Be_2 - e_1) + e_2 S_2 Pf'k')f$. In the above, primes denote derivatives and all population densities are equilibrium values. The quantity Q is equal to a negative constant multiplied by the determinant of the Jacobian matrix of equations (1) evaluated at the equilibrium. This determinant must be negative at a stable point equilibrium, implying that $Q > 0$. This implies that the equilibrium P always increases with r at a stable equilibrium. Resource density increases when the number of prey eaten per unit time by the predators increases with predator density (when $f + f'P > 0$), but will decrease if this inequality is reversed (which requires strong anti-predator behaviour and a high predator population). The equilibrium N may increase or decrease with increasing r. Prey density must increase with r when resource density decreases with r, but it also may increase over a range of values of r for which R increases (i.e. when $f + f'P$ is small and positive). If N increases for all r above a threshold value, it is clearly impossible for enrichment to cause extinction of the intraguild prey. Figure 1 provides two examples of the responses of prey and predator to increasing r when $k(R) = R$, and $f = 1/(1 + \alpha P)$, where α is a constant. This function satisfies the condition $f + f'P > 0$, but larger values of α decrease the magnitude of $f + f'P$. In this system, R (not shown) and P always increase with r, while N increases with r for large α, but decreases with r for small enough values of α. These two alternatives are illustrated in Figs. 1A and 1B. Non-monotonic responses of N to r may occur given the more general function $f = 1/(1 + \alpha P^m)$ with $m > 1$.

The general results based on equations (2) may be compared to those of the similar model that lacks prey defence by substituting 1 for f and 0 for f' in equations (2). This non-behavioural model predicts that the predator and resource increase and the prey decreases with enrichment, when the latter is modelled as a larger r. Thus, the results suggest that low or no-cost defence may alter the responses of both the resource and prey to enrichment in an IGP system, but will not change the prediction of an increase in predator density. The analysis can easily be redone using logistic density dependence, $f = r(1 - (R/K))$, assuming that enrichment increases K. The conditions giving the sign of the left-hand sides of equations (2) are identical to those for enrichment that increases r.

The responses of abundances to increased per capita mortality of the predator (d), given equations (1), can be determined using the methods employed above. The results are: (1) predator density always decreases in response to increased predator per capita mortality; (2) resource density decreases if $f + Pf' > 0$, and increases if this inequality is reversed; (3) prey density increases with d when $-e_2 BCNf' - e_1 S_1 (f + Pf') < 0$, but decreases when this inequality is reversed, i.e. when the defensive response is strong (f' is large enough in magnitude). These criteria are identical to those for the responses to lower resource growth (reduced r), which is a consequence of the important role of predator population size in determining responses to both top-down and bottom-up perturbations.

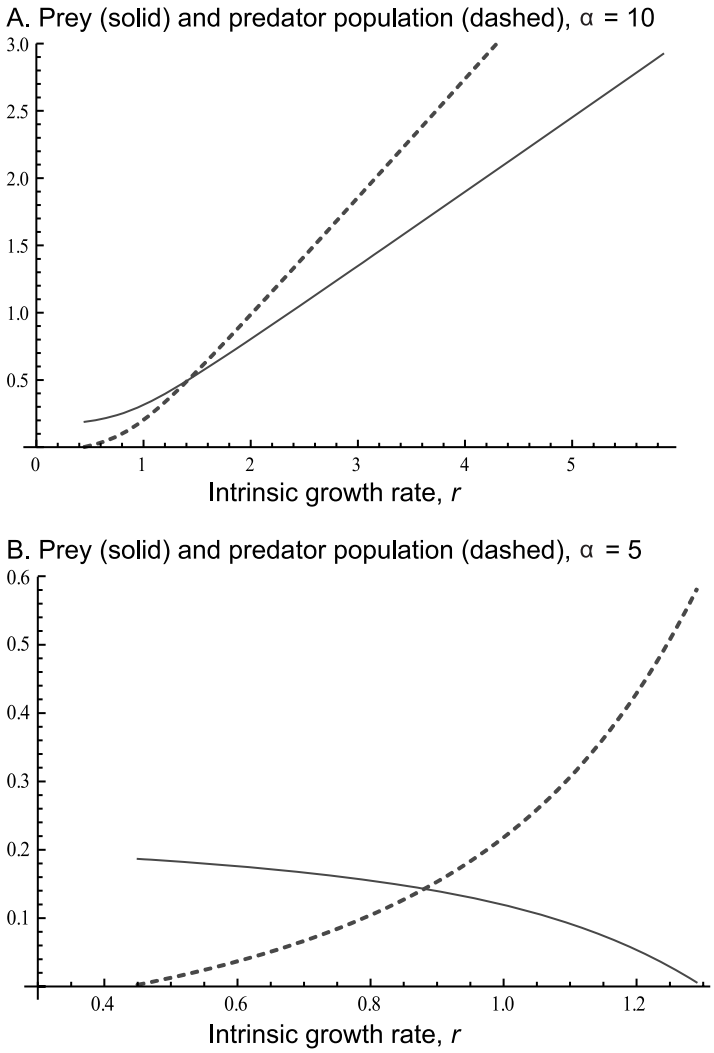

Fig. 1. Predator (dashed line) and prey (solid line) as a function of resource intrinsic growth rate, r, for a system based on equations (1) with $f = 1/(1 + \alpha P)$. The resource density dependence is logistic with $k(R) = R$. The parameter values are: $B = 0.2$; $C = 1$; $D = 0.05$; $e_1 = 0.2$; $e_2 = 0.4$; $S_1 = 0.5$; $S_2 = 1$; $d = 0.1$. In both cases, resource density (not shown) increases at a decelerating rate with increased r.

The preceding results may be compared with corresponding ones for a food chain, which is simply equations (1) with $S_1 = 0$. In this case, when defence is present ($f' < 0$) the equilibrium prey density always increases in response to higher r; N does not respond to r when defence is absent. Higher predator mortality, d, has the well-known effect of decreasing prey and increasing resource density in the absence of defence. When it is cost-free, prey density increases with predator mortality if the resulting decrease in predator density reduces total predation risk $S_2 fP$, but prey density decreases with greater predator mortality when total risk decreases with increasing P (i.e. $f + Pf' < 0$). The resource abundance always responds to predator mortality in the direction opposite to the

Table 1. Qualitative responses of food chain and IGP systems compared

	Food chain		IGP	
	bottom up	top down	bottom up	top down
1. No prey defensive behaviour				
P	+	–	+	–
N	0 (+)*	+	–	+
R	+	–	+	–
2. Cost-free defence				
P	+	–	+	–
N	+	+ or –	+ or –	+ or –
R	+ or –	+ or –	+ or –	+ or –
3. Costly defence				
P	+	–	+	–
N	+ or –	+ or –	+ or –	+ or –
R	+	–	+	–

* An increase in *N* would occur in any system that had some direct negative effects of predator density on the predator's per capita growth rate; otherwise, equilibrium prey density is not altered by enrichment.

prey's response. These and other responses to top-down and bottom-up perturbations are summarized in Table 1.

We are interested in the conditions that allow persistence of the prey in an IGP system, as well as impacts on its abundance. Persistence of the prey requires that it be able to increase when it is rare and the predator and resource are at their ultimate dynamics (in the current model, this is a stable equilibrium point). The prey invasion criterion is:

$$\frac{BCd}{e_1 S_1} - D - S_2 \frac{r - k(d/(e_1 S_1))}{S_1} f\left[\frac{r - k(d/(e_1 S_1))}{S_1}\right] > 0 \tag{3}$$

The third term in this expression is the product $S_2 Pf(P)$ at the equilibrium point. If this is a decreasing function of P (i.e. $f + Pf' > 0$), then increased resource growth, whether it involves an increased r or a decreased function k, allows prey persistence over a wider range of parameter values. If the predator dependence in the functional response to prey is weaker, prey risk ($Pf(P)$) is an increasing function of P, and the conditions that allow persistence of the prey become more stringent as productivity increases (i.e. under enrichment). Whether this ultimately results in exclusion of the prey at a high enough productivity depends on whether the product $Pf(P)$ approaches an asymptote at high productivity in a system with the prey absent. The product $Pf(P)$ approaches an asymptote of $1/\alpha$ when $m = 1$ if the function discussed above describes predator dependence (i.e. $f = 1/(1 + \alpha P)$). If the P in the denominator of this function is raised to a power greater than 1, then the predation risk to the prey decreases at a high enough value of r, and condition (3) is relaxed.

Predator density in a P–R system does not approach an asymptote when higher productivity implies increased r, but it does approach an asymptote when enrichment only affects (reduces) the function k, describing resource density dependence (e.g. when the

resource grows according to the logistic equation and carrying capacity, K, is the only parameter that increases with enrichment). Specifically, if $k(R)$ becomes very small at high productivity, then the maximum predator density in a resource–predator system is r/S_1. If the prey has a sufficiently low resource requirement and a low enough susceptibility to predation, it will be able to invade a P–R system at this predator density, so can never be excluded. Diehl and Feissel (2000) and Diehl (2003) discuss a similar result for a model without prey defence.

Systems in which prey defence is costly

D–S_2 trade-off

Facultative anti-predator behaviour is likely to involve a cost to the prey species. This may reduce the level of defence compared with a cost-free scenario but it may also alter the prey–resource relationship in a way that promotes persistence. Here we investigate models in which the prey is characterized by either higher background mortality or a lower resource consumption rate as a consequence of decreased exposure to the predator. Given the same basic framework as equations (1), defence that entails greater background mortality and is adjusted adaptively can be represented by:

$$\begin{aligned}
\frac{dR}{dt} &= R\left(r - k(R) - CN - S_1P\right)\\
\frac{dN}{dt} &= N\left(BCR - D(S_2) - S_2P\right)\\
\frac{dP}{dt} &= P\left(e_1S_1R + e_2S_2N - d\right)\\
\frac{dS_2}{dt} &= v\left(-\frac{dD}{dS_2} - P\right) + \frac{\mu}{S_2} - \frac{\mu}{S_{\max} - S_2}
\end{aligned} \qquad \text{(4a, b, c, d)}$$

where prey mortality due to causes other than predation, D, is a decreasing function of the prey's vulnerability to the predator, S_2. This reflects scenarios such as that where prey must use physiologically stressful habitats to avoid the predator. Here we assume that the second derivative of D with respect to S_2 is positive. This condition is likely because there is a lower limit to D, and is necessary if the adaptive equilibrium at intermediate S_2 is to represent a fitness maximum. Equation (4d) is a model of the dynamics of the prey vulnerability trait, S_2, using the approach of Abrams and Matsuda (2004). The parameter v is a rate constant, reflecting the general speed of adaptation, and the quantity in parentheses in equation (4d) is the gradient of individual fitness with respect to the trait. The final two terms in equation (4d) reflect the biased change in vulnerability when the trait S_2 approaches its minimum value of 0 or its maximum of $S_{2\max}$. Limitations on the predator's rate of capturing even undefended prey are expected to set this maximum. The value of μ is assumed to be several orders of magnitude less than the minimum of 1 or the adaptive rate constant, v. Thus, the two terms involving μ have little impact on trait dynamics until the trait approaches one of its limiting values. In the absence of predators, S_2 approaches $S_{2\max}$, and when predators are very abundant, S_2 can become very small. (If both mortality costs and predators were

removed, the bias terms would produce a slow approach of S_2 to $S_{2\max}/2$.) For a more detailed justification for this type of model, see Abrams and Matsuda (2004). All else being equal, the equilibrium S_2 decreases as predator abundance increases (Abrams, 1982, 1984).

The Appendix uses implicit differentiation of the equilibrium conditions for equations (4) to derive general expressions for the response of the equilibrium values of the variables to an increased resource r. The derivation assumes that the biased behaviour terms are small enough to be ignored in calculating the equilibrium. The results in the Appendix show that it is again possible for the prey to either increase or decrease with r. The direction of change in prey density with increasing resource intrinsic growth rate is given by the sign of $BCe_2N - e_1S_1S_2D''$ evaluated at the equilibrium point. Here $D'' = \partial^2 D/\partial S_2^2$. Because D'' must be > 0 at a fitness maximum, this sign-determining quantity for the prey response is the difference between two positive quantities. Prey density increases with r for large N or near linear D. For many plausible forms of the mortality rate function D, the equilibrium N is a unimodal function of r. This is true, for example, when D is assumed to have the form: $D = D_0 + D_1/S_2$. In this case, the optimal value of S_2 is $S_2 = \sqrt{D_1/P}$. Exclusion of prey at high enough productivities in this example is inevitable because the prey's mortality approaches infinity as its vulnerability to the predator approaches zero. If the death rate is finite when $S_2 = 0$, the prey will be able to persist at any level of productivity, provided resource intake, BCR^*, is greater than the maximum death rate (where R^* is the resource density at the predator–resource equilibrium). The predator and resource densities always increase with r. An analogous derivation (P.A. Abrams, unpublished) can be used to demonstrate that the same results describe the signs of the impacts of enrichment on the equilibrium values of the variables, where enrichment means increasing K in a logistic model or, more generally, reducing the magnitude of the function $k(R)$.

The impact of the predator death rate on the equilibrium densities under equations (4) may be determined using the same methods as above. In this case, the impact of predator mortality is qualitatively similar to what it would be either in the absence of intraguild predation with adaptive defence, or in the absence of defence with IGP present; higher predator mortality reduces predator and resource populations, while increasing the prey population. All of the general results for this trade-off are again summarized in Table 1.

C–S_2 trade-off

A more commonly observed trade-off (Werner and Peacor, 2003) is one in which decreased exposure to the predator implies a decreased intake of the resource for the intraguild prey. This is the final type of model considered here, and it is given by:

$$\begin{aligned}
\frac{dR}{dt} &= R\left(r - k(R) - C(S_2)N - S_1P\right)\\
\frac{dN}{dt} &= N\left(b\left[C(S_2)R\right] - D - S_2P\right)\\
\frac{dP}{dt} &= P\left(e_1S_1R + e_2S_2N - d\right)\\
\frac{dS_2}{dt} &= v\left(b'\,R\frac{dC}{dS_2} - P\right) + \frac{\mu}{S_2} - \frac{\mu}{S_{\max} - S_2}
\end{aligned} \qquad (5a, b, c, d)$$

Here the symbols have the same meanings as in equations (4); the only differences are that C rather than D is assumed to be affected by vulnerability, S_2, and the numerical response b is assumed be to an increasing but possibly non-linear function of the functional response, CR. For the behavioural equilibrium to be stable on a short time scale, it is necessary that the derivative of the right-hand side of equation (5d) be negative. If the equilibrium is not close to either 0 or $S_{\max}$, this condition is approximately $b''R^2C'^2 + b'C'' < 0$, where primes again denote derivatives with respect to the argument of the function (e.g. $C' = dC/dS_2$). The effect of increased r on the equilibrium prey abundance is analysed in the Appendix for a linear numerical response function, $b = BCR$, and for an arbitrary non-decreasing response, $b(CR)$. If b is linear, the results are relatively similar to those for the previous trade-off involving the prey death rate. Both resource and predator densities increase with r, while the response of the prey is indeterminate. If C is linear and b is non-linear, b must increase at a decelerating rate with S_2 at a stable behavioural equilibrium (Abrams, 1984). This implies that P and R increase and the equilibrium S_2 decreases with increases in the resource per capita growth, r. Prey density may again increase or decrease with r (the conditions are discussed in the Appendix). These cases of adaptive behaviour with non-linear b and/or C permit the entire system to exhibit limit cycles, so numerical analysis of specific models is needed to determine the outcome of enrichment.

The example used here is an extension of a model used previously in a study of a three-species food chain (Abrams, 1995). The prey's per capita growth function, b, has the form $B - q/(CR)$, where the equilibrium resource requirement is identical to that in the linear numerical response model of equation (1b) when $q = D$. This hyperbolic form was proposed by Getz (1993), and it avoids the unrealistic exponential decline of prey in the absence of resource. The values of C and S_2 are both assumed to be proportional to foraging time. This allows C to be expressed as C_0S_2, where C_0 is a positive constant. The behavioural variable is S_2; if this changes rapidly relative to predator and resource densities, it takes on a value that maximizes $B - q/(C_0S_2R) - S_2P$, i.e. $S_2 = \sqrt{q/(C_0PR)}$. Because this produces a decelerating (type-2) consumer functional response, the system may exhibit limit cycles, even when the predator density is fixed. Figure 2A shows how both prey and predator change as a function of increased K for a particular set of parameters. Both species increase with K when the system is stable, and both decrease with K when the system starts to undergo limit cycles. Above approximately $K = 10$, the predator increases and the prey continues to decrease. This corresponds to a range of carrying capacities that is sufficient to allow the predator to exist on the resource alone.

The pattern shown in Fig. 2A is sensitive to the shape of the predator's numerical response, which determines how the cycles generated by the prey affect average predator per capita growth rate. Figure 2B differs from the example in Fig. 2A in that the predator's numerical response has the same non-linear form as the prey; the predator's per capita growth rate is $1 - d/(e_1S_1R + e_2S_2N)$. Once again, this does not alter equilibrium densities compared with the system shown in Fig. 2A, but it has a major effect on the cycles that occur in unstable systems. In this case, there is a significant range of carrying capacities over which the mean N increases and the mean P decreases; predator and prey decrease when K becomes sufficiently high, but the prey persists at all values of K. Results for increasing r rather than K in this example are similar except that the amplitude of cycles becomes extremely large at a moderately large r; at low values of r yielding stable dynamics, all three species increase with r.

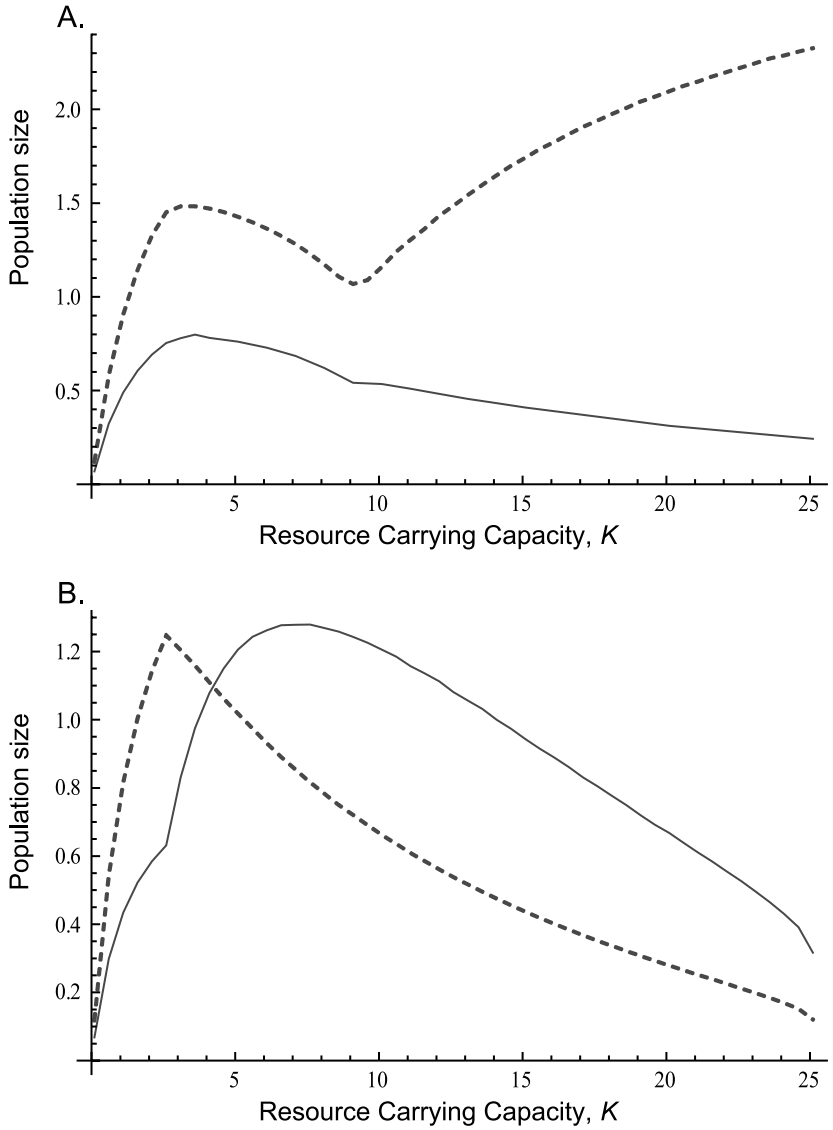

Fig. 2. Predator and prey densities as a function of the resource carrying capacity in the IGP system described in the text as an example of equation (5). The parameter values are: $r = 1$; K given on x-axis; $I = 0.001$; $B = 4$; $C_0 = 0.2$; $q = 0.5$; $S_1 = 0.3$; $e_1 = 0.3$; $e_2 = 0.6$; $d = 0.7$. The solid line shows the prey and the dashed line is the predator. See text for more details. Panel (A) assumes a linear numerical response for the predator, while panel (B) assumes that the predator, like the prey, has the type of hyperbolic numerical response advocated by Getz (1993; see also Abrams, 1995). In panel (A), the change in the population trajectories between $r = 9$ and $r = 10$ corresponds to a transition from period-1 to period-2 cycles. In panel (B), the change in trajectories near $r = 3$ corresponds to the transition from a stable equilibrium to limit cycles.

More generally, the ability of the prey to persist in productive systems is equivalent to its ability to invade the predator–resource equilibrium in such systems. This invasion ability may be measured by the maximum prey death rate that allows invasion: $D_{\max} = \max[b(CR^*) - S_2P^*]$, where R^* and P^* denote the equilibrium values in the absence of the consumer, and the maximum of prey fitness is taken over the range of possible values of S_2. Because $R^* = d/(e_1S_1)$ and $P^* = (1/S_1)[r - k(d/(e_1S_1))]$, higher resource productivity (increased r and/or decreased k) increases P^* without changing R^*. It follows directly that $D_{\max}$ decreases as resource productivity increases. However, if there is an asymptotic maximum r at high productivity, there is also a maximum P^*, and $D_{\max}$ then approaches an asymptote as productivity becomes very high. This means that prey having a per capita mortality D lower than $D_{\max}$ can persist at all levels of enrichment.

The responses of equilibrium values of the four variables in equations (5) to predator mortality can be determined using the same general approach used for enrichment. The results are given in the Appendix (and Table 1). These show that predator and resource abundances both decline in response to increased predator mortality when the equilibrium of the system is stable. Once again, the response of the prey is indeterminate, and cases with limit cycles or more complex dynamics must be explored numerically. In this case, the criterion giving the sign of the prey response is sufficiently complicated to require numerical analysis even in most stable cases.

Examination of a more general three-species model with both non-linear functional and numerical responses would require extensive numerical analysis to determine both invasion conditions and responses of population sizes to enrichment and predator mortality. However, the models with linear functional responses analysed here are sufficient to show that adaptive defence frequently alters the response of prey density to environmental variables. Defence often makes prey persistence more likely than in comparable models that lack defence, and it makes an increase in prey density possible in response to either increased resource productivity or decreased predator mortality. A summary of the responses of equilibrium densities to perturbations for the IGP models considered here, and a comparison with food chain models, is provided in Table 1.

Other IGP systems

The modelling framework considered here fails to include many features that characterize most real systems. Perhaps most important is its restriction to the three-species system that has been the subject of most modelling in the IGP literature. It is questionable whether any natural system can be characterized as having a single resource (Abrams, 1988), and it is likely that resource partitioning between the predator and prey exists in IGP systems. Predators are likely to have several prey (Cohen *et al.*, 1990), and preliminary explorations suggest that significant differences exist between the simple three-species system considered here (and in most of the IGP literature) and systems with more species (for analysis of some larger systems, see Fussmann and Heber, 2002; Daugherty *et al.*, 2007; Holt and Huxel, 2007; Namba *et al.*, 2008). There is insufficient space to address the many potential impacts of additional species here. However, it is clear that adaptive defence by the prey can have a greater range of impacts in such larger models. Higher-level predators can limit the increase in the intraguild predator that would otherwise accompany enrichment. The presence of a second resource used exclusively by the prey not only limits the competitive impact of the intraguild predator on the prey (Holt and Huxel, 2007), but it also provides another mechanism by which prey density can be increased by greater

predator densities. If greater risk reduces the prey's attack rate on all of its resources, it will often reduce over-exploitation of the exclusively used resource(s). This can cause the prey to increase in response to greater predation risk, whether it is generated by top-down or bottom-up perturbations.

DISCUSSION

Many previous models (see Introduction) have suggested that enriching the basal resource in an IGP system is likely to decrease the abundance of the prey species, and that sufficiently high levels of enrichment will result in the prey's exclusion. Although top-down effects in IGP systems have received less attention, Polis and Strong's (1996) suggestion that intraguild predation inhibits trophic cascades is frequently cited. Adaptive defence by prey has an impact on the responses of abundances to both types of environmental change. Defence makes it more likely that prey abundance will increase over a range of productivities, and defence also often increases the range of conditions when the prey cannot be excluded by high resource productivity. Defence can alter the responses of trophic level abundances to top-down perturbations in IGP systems and lead to predators and resources changing in opposite directions in response to such a perturbation. This is in part because the direction of response of prey density to a top-down perturbation also becomes indeterminate in the presence of adaptive prey defence. This possibility is not unique to food webs with intraguild predation. Abrams and Vos (2003) explored conditions that allow a prey species to increase in response to decreased mortality of their predator in a three-species food chain with adaptive defence.

The models analysed here differ in whether there is or is not a cost to the prey's defensive behaviour. The main results suggest that such a cost has its largest impact on the response of the resource to top-down and bottom-up perturbations. In models based on adaptive balancing of costs and benefits by the prey, the resource and predator densities changed in the same direction in response to a top-down or bottom-up perturbation, and it is the direction predicted by simple models of food chains (Oksanen *et al.*, 1981). In the first model, which reflects cost-free defence, resource density could decline in response to resource enrichment or lower predator mortality. When this occurs, the responses of predator and resource abundances to either predator mortality or resource enrichment are in opposite directions. Costs of defence alter the conditions under which prey increase or decrease in response to a perturbation, but do not alter the fact that both directions of response are possible.

The idea that anti-predator behaviour might affect the outcome of intraguild predation is not new, having been mentioned in a short paragraph in the discussion of Holt and Polis (1997). However, this suggestion has received remarkably little attention, either theoretically or empirically. One exception is the work of Amarasekare (2006, 2007b) on IGP meta-communities. In her studies, some of the predictions of simpler models are altered in part because species are able to reduce risk of predation by movement to patches with fewer predators. Amarasekare showed that the total prey population may increase in response to increased productivity in such a system. However, this is a rather specific kind of anti-predator behaviour. It also has the special characteristic that the protection afforded by a new habitat is often temporary, as predators eventually increase in abundance in that habitat due to movement and/or reproduction. The one theoretical treatment of defence that is not tied to spatial location seems to have been the study of Kimbrell *et al*. (2007). These

authors analysed a model of intraguild predation in which either or both of the two lower-level species could exhibit 'vigilance', which reduced their susceptibility to predation according to a hyperbolic function and reduced their maximum per capita growth rate linearly. In addition to assuming specific functional forms for the costs and benefits of vigilance, Kimbrell and colleagues' analysis also focused on the question of whether the top predator could persist if it killed, but did not consume, the intermediate species. They did not explore the impact of enrichment on prey persistence.

The results presented here confirm that adaptive defence by the prey in a simple three-species IGP system can result in prey density increasing with productivity, and may also prevent prey exclusion at high productivities. These are the patterns most often cited as areas of conflict between simple theory on intraguild predation and empirical observation (Amarasekare, 2008). Lake ecosystems have provided evidence for both patterns: increases in all trophic levels with enrichment (Ginzberg and Akçakaya, 1992) and extensive intraguild predation (Sprules and Bowerman, 1988; Vadeboncoeur *et al.*, 2005). There have also been many studies of adaptive defence and foraging in such systems (for reviews, see Lima, 1998; Werner and Peacor, 2003). The positive effects of prey defence are especially likely to be observed in systems with additional mechanisms that limit the increase in predator population density that would otherwise occur at very high productivity. These mechanisms include density-dependent reductions in predator per capita growth rate due to factors other than food (Hart, 2002; Amarasekare, 2007a, 2008), and cycling of the predator due to a saturating functional response (Abrams and Fung, in press).

The literature on intraguild predation has emphasized differences between such systems and those, such as food chains, in which trophic levels are more distinct (Holt and Polis, 1997). While there are clearly some differences, the range of potential responses to top-down and bottom-up perturbations in models with realistic complications, such as adaptive prey defence, largely overlap. Table 1 shows that the range of different top-down and bottom-up responses of food chains and IGP systems, given the most probable type of trade-off (C vs. S_2), are identical except for the possibility of prey decline in response to enrichment in the IGP system. The presence or absence of intraguild predation in a food web may have fewer system-wide consequences than the simplest previous models suggested. Fussmann and Heber (2002) found relatively small differences in proportions of different types of dynamics in larger webs with and without intraguild predation. Our analysis compares a model in which defence has no cost to analogous models in which defence reduces another component of prey fitness. Although costs of defence have some effect, our models of both costly and cost-free defence share the basic result that defence makes the response of prey abundance to increased productivity indeterminate in direction. The presence of costs in our model rules out the possibility of an increase in equilibrium resource density in response to increased predator mortality, which may occur with cost-free defence. This finding is important for assessing whether additional biological control agents (which often exhibit intraguild predation) are likely to increase pest (resource) densities (see Okuyama, 2009).

ACKNOWLEDGEMENTS

This work was supported by an NSERC Discovery Grant to P.A.A. and an NSERC Postgraduate Scholarship to S.R.F. We appreciate comments by R.D. Holt and S. Diehl on earlier drafts of some of the ideas presented here.

REFERENCES

Abrams, P.A. 1982. Functional responses of optimal foragers. *Am. Nat.*, **120**: 382–390.

Abrams, P.A. 1984. Foraging time optimization and interactions in food webs. *Am. Nat.*, **124**: 80–96.

Abrams, P.A. 1988. How should resources be counted? *Theor. Popul. Biol.*, **33**: 226–242.

Abrams, P.A. 1992. Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptations. *Am. Nat.*, **140**: 573–600.

Abrams, P.A. 1993. Why predation rates should not be proportional to predator density. *Ecology*, **74**: 726–733.

Abrams, P.A. 1994. The fallacies of 'ratio-dependent' predation. *Ecology*, **75**: 1842–1850.

Abrams, P.A. 1995. Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. *Am. Nat.*, **146**: 112–134.

Abrams, P.A. 2009. Determining the functional form of density dependence: deductive approaches for consumer–resource systems with a single resource. *Am. Nat.*, **174**: 321–330.

Abrams, P.A. 2010. Implications of flexible foraging for interspecific interactions: lessons from simple models. *Funct. Ecol.*, **24**: 7–17.

Abrams, P.A. and Fung, S.R. in press. Prey persistence and abundance in systems with intraguild predation and type-2 functional responses. *J. Theor. Biol.* (DOI: 10.1016/j.jtbi.2010.02.045).

Abrams, P.A. and Ginzburg, L.R. 2000. Models of predation: prey dependent, ratio dependent or neither? *Trends Ecol. Evol.*, **15**: 337–341.

Abrams, P.A. and Matsuda, H. 1997. Prey evolution as a cause of predator–prey cycles. *Evolution*, **51**: 1740–1748.

Abrams, P.A. and Matsuda, H. 2004. Consequences of behavioral dynamics for the population dynamics of predator–prey systems with switching. *Pop. Ecol.*, **46**: 13–25.

Abrams, P.A. and Vos, M. 2003. Adaptation, density dependence, and the abundances of trophic levels. *Evol. Ecol. Res.*, **5**: 1113–1132.

Abrams, P.A., Matsuda, H. and Harada, Y. 1993. Evolutionarily unstable fitness maxima and stable fitness minima in the evolution of continuous traits. *Evol. Ecol.*, **7**: 465–487.

Amarasekare, P. 2006. Productivity, dispersal and the coexistence of intraguild predators and prey. *J. Theor. Biol.*, **243**: 121–133.

Amarasekare, P. 2007a. Trade-offs, temporal variation, and species coexistence in communities with intraguild predation. *Ecology*, **88**: 2720–2728.

Amarasekare, P. 2007b. Spatial dynamics of communities with intraguild predation: the role of dispersal strategies. *Am. Nat.*, **170**: 819–831.

Amarasekare, P. 2008. Coexistence of intraguild predators and prey in resource-rich environments. *Ecology*, **89**: 2786–2797.

Arim, M. and Marquet, P.A. 2004. Intraguild predation: a widespread interaction related to species biology. *Ecol. Lett.*, **7**: 557–564.

Bolker, B., Holyoak, M., Křivan, V., Rowe, L. and Schmitz, O.J. 2003. Connecting theoretical and empirical studies of trait-mediated interactions. *Ecology*, **84**: 1101–1114.

Brown, J.S., Laundre, J.W. and Gurung, M. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *J. Mammal.*, **80**: 385–399.

Cohen, J.E., Briand, F. and Newman, C.M. 1990. *Community Food Webs: Data and Theory*. New York: Springer-Verlag.

Daugherty, M.P., Harmon, J.P. and Briggs, C.J. 2007. Trophic supplements to intraguild predation. *Oikos*, **116**: 662–677.

DeAngelis, D.L., Goldstein, R.A. and O'Neill, R.V. 1975. A model for trophic interaction. *Ecology*, **56**: 881–892.

Diehl, S. 2003. The evolution and maintenance of omnivory: dynamic constraints and the role of food quality. *Ecology*, **84**: 2557–2567.

Diehl, S. and Feissel, M. 2000. Effects of enrichment on three-level food chains with omnivory. *Am. Nat.*, **155**: 200–218.

Fryxell, J.M. and Lundberg, P. 1998. *Individual Behaviour and Community Dynamics*. London: Chapman & Hall.

Fussmann, G.F. and Heber, G. 2002. Food web complexity and chaotic population dynamics. *Ecol. Lett.*, **5**: 394–401.

Getz, W.M. 1993. Metaphysiological and evolutionary dynamics of population exploiting constant and interactive resources: *r–K* selection revisited. *Evol. Ecol.*, **7**: 287–305.

Ginzberg, L.R. and Akçakaya, H.R. 1992. Consequences of ratio-dependent predation for steady-state properties of ecosystems. *Ecology*, **73**: 1536–1543.

Gismervik, I. and Andersen, T. 1997. Prey switching by *Acartia clausi*: experimental evidence and implications of intraguild predation assessed by a model. *Mar. Ecol. Progr. Ser.*, **157**: 247–259.

Hart, D.R. 2002. Intraguild predation, invertebrate predators and trophic cascades in lake food webs. *J. Theor. Biol.*, **218**: 111–128.

Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.*, **91**: 385–398.

Holt, R.D. and Huxel, G.R. 2007. Alternative prey and the dynamics of intraguild predation: theoretical perspectives. *Ecology*, **88**: 2706–2712.

Holt, R.D. and Polis, G.A. 1997. A theoretical framework for intraguild predation. *Am. Nat.*, **149**: 745–764.

Kimbrell, T., Holt, R.D. and Lundberg, P. 2007. The influence of vigilance on intraguild predation. *J. Theor. Biol.*, **249**: 218–234.

Kooi, B.W., Kuijper, L.D.J., Boer, M.P. and Kooijman, S.A.L.M. 2002. Numerical bifurcation analysis of a tri-trophic food web with omnivory. *Math. Biosci.*, **177/178**: 201–228.

Křivan, V. 2000. Optimal intraguild foraging and population stability. *Theor. Popul. Biol.*, **58**: 79–94.

Křivan, V. and Diehl, S. 2005. Adaptive omnivory and species coexistence in tri-trophic food webs. *Theor. Popul. Biol.*, **67**: 85–99.

Kuijper, L.D.J., Kooi, B.W., Zonneveld, C. and Kooijman, S.A.L.M. 2003. Omnivory and food web dynamics. *Ecol. Model.*, **163**: 19–32.

Lima, S.L. 1998. Stress and decision-making under risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Adv. Stud. Behav.*, **27**: 215–290.

Lima, S.L. and Dill, L. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, **68**: 619–640.

Moehrenschlager, A., List, R. and Macdonald D.W. 2007. Escaping intraguild predation: Mexican kit foxes survive while coyotes and golden eagles kill Canadian swift foxes. *J. Mammal.*, **88**: 1029–1039.

Mylius, S.D., Klumpers, K., de Roos, A.M. and Persson, L. 2001. Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *Am. Nat.*, **158**: 259–276.

Namba, T., Tanabe, K. and Maeda, N. 2008. Omnivory and stability of food webs. *Ecol. Complex.*, **5**: 73–85.

Oksanen, L., Fretwell, S.D., Arruda, J. and Niemela, P. 1981. Exploitation ecosystems in gradients of primary productivity. *Am. Nat.*, **118**: 240–261.

Okuyama, T. 2009. Intraguild predation in biological control: consideration of multiple resource species. *BioControl*, **54**: 3–7.

Peacor, S.D. 2002. Positive effects of predators on prey growth rate through induced modifications of prey behavior. *Ecol. Lett.*, **5**: 77–85.

Polis, G.A. and Strong, D.R. 1996. Food web complexity and community dynamics. *Am. Nat.*, **147**: 813–846.

Rosenheim, J.A. 2007. Intraguild predation: new theoretical and empirical perspectives. *Ecology*, **89**: 2679–2680.

Skalski, G.T. and Gilliam, J.F. 2001. Functional responses with predator interference: viable alternatives to the Holling type II model. *Ecology*, **82**: 3083–3092.

Sprules, W.G. and Bowerman, J.E. 1988. Omnivory and food chain length in zooplankton food webs. *Ecology*, **69**: 418–426.

Vadeboncoeur, Y., McCann, K.S., Vander Zanden, M.J. and Rasmussen, J.B. 2005. Effects of multi-chain omnivory on the strength of trophic control in lakes. *Ecosystems*, **8**: 682–693.

van de Wolfshaar, K.E., de Roos, A.M. and Persson, L. 2006. Size-dependent interactions inhibit coexistence in intraguild predation systems with life-history omnivory. *Am. Nat.*, **168**: 62–75.

Werner, E.E. and Peacor, S.D. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology*, **84**: 1083–1100.

APPENDIX

Impact of productivity on the equilibrium values of variables in systems with costly defence

Equations (4) in the text assume that increased defence implies higher mortality from other causes. By setting the left-hand sides of equations (4a–d) to zero, implicitly differentiating the resulting equations with respect to r, and solving for the four partial derivatives of equilibrium values of the variables with respect to r yields:

$$\frac{\partial R}{\partial r} = \frac{e_2 S_2^2 D''}{BC^2 e_2 N + S_2\left(CS_1(Be_2 - e_1) + e_2 S_2 k'\right)D''}$$

$$\frac{\partial P}{\partial r} = \frac{BCe_2 S_2 D''}{BC^2 e_2 N + S_2\left(CS_1(Be_2 - e_1) + e_2 S_2 k'\right)D''} \qquad \text{(A1a, b, c, d)}$$

$$\frac{\partial N}{\partial r} = \frac{BCe_2 N - e_1 S_1 S_2 D''}{BC^2 e_2 N + S_2\left(CS_1(Be_2 - e_1) + e_2 S_2 k'\right)D''}$$

$$\frac{\partial S_2}{\partial r} = \frac{-BCe_2 S_2}{BC^2 e_2 N + S_2\left(CS_1\,(Be_2 - e_1) + e_2 S_2 k'\right)D''}$$

Here $D'' = \partial^2 D/\partial S_2^2$, which is itself a function of S_2; similarly, $k' = \partial k/\partial N$, which is a function of N. The denominator of all of the four expressions must be positive based on the stability conditions for the equilibrium. The second derivative of the prey's death rate function (D'') must be positive for the equilibrium value of S_2 to represent a fitness maximum. These two conditions imply that R and P increase with r, while the prey's vulnerability to the predator, S_2, decreases. The prey density, N, may either increase or decrease with r; the sign of equation (A1c) is determined by its numerator, and is generally positive when N is sufficiently large or when the function D is sufficiently close to linear.

If C rather than D is a function of S_2, the same methods may be applied to equations (5) in the text, producing the following set of derivatives:

$$\frac{\partial R}{\partial r} = \frac{-C''e_2S_2^2R}{C^2e_2N - CS_2\left(2C'e_2N + C''RS_1(Be_2 - e_1)\right) + Ne_2C'^2S_2^2 - C''k'e_2S_2^2R}$$

$$\frac{\partial P}{\partial r} = \frac{-BCC''e_2S_2R}{C^2e_2N - CS_2\left(2C'e_2N + C''RS_1(Be_2 - e_1)\right) + Ne_2C'^2S_2^2 - C''k'e_2S_2^2R} \qquad \text{(A2a, b, c, d)}$$

$$\frac{\partial N}{\partial r} = \frac{e_2N(C - C'S_2) + C''e_1S_1S_2R}{C^2e_2N - CS_2\left(2C'e_2N + C''RS_1(Be_2 - e_1)\right) + Ne_2C'^2S_2^2 - C''k'e_2S_2^2R}$$

$$\frac{\partial S_2}{\partial r} = \frac{-e_2S_2(C - C'S_2)}{C^2e_2N - CS_2\left(2C'e_2N + C''RS_1(Be_2 - e_1)\right) + Ne_2C'^2S_2^2 - C''k'e_2S_2^2R}$$

In this case, the denominators are again proportional to the determinant, and must be positive at a stable equilibrium. The second derivative of C with respect to S_2 (i.e. C'') must be negative if the equilibrium C is to represent a fitness maximum. This implies that R and P must increase with increased productivity. Because C must increase with S_2 at a decelerating rate at a stable behavioural equilibrium, the factor $C - C'S_2$ will often be positive [this is true, for example, if $C(S_2)$ has the form of a Holling (1959) 'disk equation' function, or is a power function with an exponent < 1]. In this case, S_2 decreases as r increases, and N will increase with r if the numerator of equation (A2c) is positive (e.g. if N is large relative to R or if e_2 is large enough relative to e_1). Note that a large enough resource capture rate, C, when vulnerability, S_2, is near zero also implies $C - C'S_2$ is positive, so S_2 decreases with r and N may increase with r.

The final modification makes the numerical response an increasing function, $b(CR)$, rather than being directly proportional to resource intake rate, CR. This results in the following changes to equations (A2):

$$\frac{\partial R}{\partial r} = \frac{-e_2S_2^2R(b'C'' + Rb''C'^2)}{Z}$$

$$\frac{\partial P}{\partial r} = \frac{-e_2S_2RCb'(b'C'' + Rb''C'^2)}{Z} \qquad \text{(A3a, b, c, d)}$$

$$\frac{\partial N}{\partial r} = \frac{b''RS_2C'(e_1S_1RC' - e_2CN) + b'\left(e_2N(C - S_2C') + e_1S_1RS_2C''\right)}{Z}$$

$$\frac{\partial S_2}{\partial r} = \frac{-e_2S_2[b'(C - S_2C') - CC'RS_2b'']}{Z}$$

where Z is again a positive quantity proportional to the determinant of the Jacobian matrix. Z reduces to b' multiplied by the denominator of the equation (A2) expressions when the numerical response is linear ($b'' = 0$). If b is non-linear, the fact that $b'C'' + Rb''C'^2 < 0$ at a stable (fitness-maximizing) behavioural equilibrium means that the equilibrium values of

both R and P increase with productivity. S_2 decreases with productivity unless the second derivative of b has a large negative magnitude. Once again, prey abundance may increase or decrease with r. In the case of a linear C where $C(0) = 0$, the sign of $\partial N/\partial r$ has the opposite sign of the term $(e_1 S_1 RC' - e_2 CN)$, which may be positive or negative. When $C(0) > 0$, the response of N to r is more likely to be positive.

Using the same model (equations 5) to determine the responses of variables to increased predator mortality yields the following results. The sign of the responses of both the equilibrium resource and predator densities to increased d may be shown to have the sign of $b'C'' + RC'^2 b''$, and, as noted above, this must be negative to have a stable behavioural equilibrium when population densities are constant. The response of N to greater predator mortality has the sign of the following, which may be positive or negative:

$$RS_2 C'^2 b''(CN - Rk') - CRS_1 C'' b'^2 - b'[CC'N + C'^2 (CR^2 S_1 b'' - S_2 N) + S_2 Rk' C''] \quad \text{(A4)}$$