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Intraguild predation and interspecific co-existence between predatory endotherms

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ABSTRACT

Background: According to the current predominant view, intraguild predation leads to the replacement of intermediate predators from highly productive habitats, whereas top predators and intermediate predators can co-exist in habitats with intermediate primary productivity. These predictions are contradicted by the observed abundance of intermediate predators in productive environments. But the predictions are derived by modelling interactions in food chains where the top predator is primarily adapted to exploit intermediate predators but also has some capacity to exploit the resources of the intermediate predators. We call this 'food chain omnivory'. In contrast, 'genuine intraguild predation' is the case where the two predators have shared tactics of resource acquisition, resulting in broadly overlapping prey preferences – that is, the interacting predators belong to the same guild as defined by Root (1967).

Questions: What are the effects of productivity on genuine intraguild predation? Do the predictions for food chain omnivory apply also to genuine intraguild predation?

Methods: We modelled genuine intraguild predation by using parameter values such that the intermediate predator and the basal prey were equally valuable to the top predator. We assumed that the basal prey was a herbivore, with a carrying capacity directly proportional to primary productivity and a habitat-specific intrinsic rate of population growth that increases asymptotically in response to increasing primary productivity.

Results: With the above premises, intermediate predators can prevail even in highly productive habitat. Also, a priority effect is possible. Predictable replacement of intermediate predators by top predators requires that intermediate predators are much easier to find than basal prey. Stable co-existence requires biologically implausible parameter values.

Conclusions: Genuine intraguild predation is a destabilizing force in food webs. The dynamics of genuine intraguild predation systems differ from those in food chain omnivory systems where the intermediate and top predators have different feeding tactics and, therefore, different prey preferences.

Keywords: co-existence, exclusion, food chain intraguild predation, omnivory, predation priority effect, stoat, weasel.

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INTRODUCTION

Predators often attack all suitable prey items, including smaller predators (Polis and McCormick, 1986; Korpimäki and Norrdahl, 1989; Polis *et al.*, 1989; Palomares and Caro, 1999; Arim and Marquet, 2004; Sergio and Hiraldo, 2008). The consequences of such predatory interactions, referred to as 'food chain omnivory' [FCO (Pimm and Lawton, 1978; Pimm, 1991)] or intraguild predation [IGP (Polis and McCormick, 1986; Polis *et al.*, 1989)], have been the subject of a long-lasting research interest, ranging from problems of co-existence (Pimm and Lawton, 1978) to the discreteness of trophic levels (Cousins, 1987; Polis and Strong, 1996).

Analyses of food chain omnivory/intraguild predation (Pimm and Lawton, 1978; Polis *et al.*, 1989; Holt and Polis, 1997; Diehl and Feißel, 2000; Mylius *et al.*, 2001; Borer *et al.*, 2003, 2007; Snyder *et al.*, 2005; Takimoto *et al.*, 2007) have shown that a top predator and an intermediate predator exploiting the same basal prey might co-exist in habitats with intermediate productivity but the zone of co-existence may be partially or entirely replaced by a zone of priority effect (Holt and Polis, 1997; Diehl and Feißel, 2000; Mylius *et al.*, 2001; Snyder *et al.*, 2005; Takimoto *et al.*, 2007; Amarasekare, 2008). In productive habitats, top predators are predicted to eliminate intermediate predators.

In apparent contrast with the predictions of FCO/IGP models, small intermediate predators abound in productive habitats, in spite of periodically heavy intraguild predation (Mikkola, 1983; Korpimäki and Norrdahl, 1989; Donaldio and Buskirk, 2006; Amarasekare, 2008). Sometimes, their numbers are suppressed by intraguild predation (Crooks and Soule, 1999; Ritchie and Johnson, 2009), but there are also productive habitats where the smallest predator species has higher densities than its bigger competitors. An example of such a community is shown in Table 1, which summarizes the abundances of different predators in a productive agricultural landscape in western Finland.

Conceptual problems may contribute to the apparent discrepancy between theory-based predictions and empirical facts. Root (1967) defined guilds as 'sets of species exploiting the same class of resources, using similar foraging tactics'. In the context of intraguild predation, however, Polis *et al.* (1989, p. 298) used a broader concept, where a guild 'included all

Table 1. The densities (individuals per km^2) and mean body weights of main mammalian and avian predators and their mammalian prey at Alajoki study area (50 km^2) in late winter (early March, mammalian predators) and early spring (late April and early May, avian predators) during 1984–1987

Year:	1984	1985	1986	1987	Source
Phase of the vole cycle:	Low	Increase	Decrease	Low	
Least weasel (42 g)	3.6	3.7	13.0	2.4	1
Stoat (141 g)	0.3	1.7	2.4	0.5	2
Eurasian kestrel (207 g)	0.08	0.68	1.96	0.77	3
Short-eared owl (315 g)	0.08	0.98	2.09	0.12	3
Long-eared owl (308 g)	0.08	0.26	0.90	0.08	3
Red fox (5300 g)	0.15	0.03	0.00	0.11	4
Microtus spp. (24 g)	40	1980	1710	200	3
Bank vole (17 g)	30	330	220	210	3
Common shrew (8 g)	1200	450	480	190	3

Source: 1 = Korpimäki and Norrdahl (1989), 2 = Korpimäki *et al.* (1991), 3 = Korpimäki and Norrdahl (1991), 4 = unpublished data of E. Korpimäki.

taxa in a community that use similar resources and thus may compete, regardless of differences in tactics of resource acquisition'. The empirical systems, used as frameworks of reference in IGP/FCO models, do not conform to the original guild concept. Diehl and Feißel (2000) studied interactions between bacteriovorous and primarily predacious ciliates, which could prey on bacteria, too. (They also used the term 'food chain omnivory', instead of intraguild predation.) Mylius *et al.* (2001) focused on interactions between zooplankters, planktivorous roaches, and primarily piscivorous perches, with some capacity to exploit zooplankters. Borer *et al.* (2003) studied a system consisting of herbivorous scale insects, endoparasitoids, and ectoparasitoids (facultative hyperparasitoids), which were assumed to be more efficient in attacking parasitized than non-parasitized scale insects. None of these cases dealt with predators belonging to the same guild, as defined by Root (1967).

The difference between a broad and a narrow guild concept matters, because co-existence and replacement in IGP/FCO systems depend on the net impact of the extra trophic step, involving the intermediate predator, on the energy balance of the top predator (Takimoto *et al.*, 2007). The only way for the longer pathway to be more profitable than the shorter one is if the foraging tactics of the top predator are best suited for catching intermediate predators, not the shared basal prey, i.e. that the interacting predators do not belong to the same guild, as defined by Root (1967). Predictions concerning replacement and co-existence have so far been deduced from generalized FCO models. These models encompass all situations where two predator species exploit one (or more) of the same prey species and where one predator also feeds on the other predator. This covers a very wide range of trophic interactions and the predators can be very different ecologically.

In the present paper, we analyse only a subset of these interactions, which we define as 'genuine intraguild predation' where the two predators belong to the same guild – in the strictest definition of that term. In genuine intraguild predation, the two predators share tactics of resource acquisition. Henceforth, we will use the term intraguild predation only in this restricted sense. We analyse how intraguild predation responds to increasing primary productivity. Other interactions combining aspects of predation and competition will be referred to as food chain omnivory.

Our focal empirical system consists of voles (*Microtus* spp.), northern least weasels (*Mustela nivalis nivalis*), and stoats (*Mustela erminea*) (for mean body weights, see Table 1). This was the first system in which genuine intraguild predation was proposed as a mechanism for interspecific co-existence (Rosenzweig, 1966). Moreover, arvicoline rodents reproduce at exceptionally high rates. They can therefore support higher densities of intermediate predators than other herbivorous endotherms, making the system maximally favourable for the invasion of the top predator.

We will perform our analysis on a parameter plane, where the x-axis is the prey's carrying capacity (K) and the y-axis is its habitat-specific intrinsic per capita rate of population growth (r). Our previous studies of the responses of plant-based food chains to increasing primary productivity (Oksanen *et al.*, 1981; Oksanen and Oksanen, 2000) show that increasing primary productivity first increases the value of r (due to increased maximum foraging rates), but the functional response of the herbivore is gradually saturated. Therefore, r converges asymptotically towards a maximum value, r_{max}. Carrying capacity, K (i.e. the density of herbivores at the plant–herbivore equilibrium), increases linearly with increasing primary productivity. Along gradients of increasing primary productivity, r and K must thus increase in concert along a 'r vs. K track', starting from the origin (i.e. habitats too barren to sustain herbivores) and rising asymptotically towards r_{max}.

MODEL STRUCTURE AND PARAMETERS

Like Diehl and Feißel (2000), we assume logistic population growth for the herbivorous basal prey [for motivation, see Hanski (1990), Berryman (1992)]. Moreover, we assume that both predators have type II functional responses (Murdoch, 1973; Hayes and Harestad, 2000; Sundell *et al.*, 2000; Oksanen *et al.*, 2001). Applying the Lotka-Volterra-Rosenzweig model structure (see Rosenzweig, 1977) to these assumptions, the rates of population growth of the basal prey (H), the intermediate predator (C), and the top predator (P) will be governed by equations (1), (2), and (3), respectively.

$$\frac{dH}{dt} = rH\left(1 - \frac{H}{K}\right) - \frac{a_c CH}{1 + a_c hH} - \frac{a_p PH}{1 + a_p \eta H + \alpha \eta C} \tag{1}$$

$$\frac{dC}{dt} = \frac{b a_c HC}{1 + a_c hH} - \frac{\alpha PC}{1 + a_p \eta H + \alpha \eta C} - mC \tag{2}$$

$$\frac{dP}{dt} = \frac{\beta a_p HP}{1 + a_p \eta H + \alpha \eta C} + \frac{\beta \alpha CP}{1 + a_p \eta H + \alpha \eta C} - \mu P \tag{3}$$

Parameters a_c and a_p represent the searching efficiencies of intermediate predators and top predators, respectively, for the basal prey; α is the searching efficiency of the top predator for the intermediate predator. Parameters m and μ are the per capita mortality rates of starving intermediate and top predators, respectively. Parameters h and η are their per prey handling times. Parameters b and β are the energetic values of ingested prey to energy for the intermediate and the top predator, respectively, expressed as fractions of daily energy needs. As the top predator must be the bigger one, we assume that $\beta < b$. We assume that both predators are equally efficient in searching for basal prey ($a_c = a_p$), have similar mortality rates when starving ($m = \mu$), and similar handling times ($h = \eta$), but we use different symbols for them for the sake of conceptual clarity.

We infer the position of the r vs. K track in the parameter plane from the data of Myllymäki (1977), Turchin and Ostfeld (1997), and Klemola *et al.* (2000). We assume that the maximum daily per capita rate of population growth of boreal and north temperate voles is about 0.016. This rate has been observed in productive fields that support about 400 voles per hectare. The track must thus pass through the point ($K = 400$, $r = 0.016$), where the curve flattens out.

In our first analysis, we assume that the searching efficiencies of the top predator for the basal prey and the intermediate predator are equal ($a_p = \alpha$). This requires that the intermediate predator, which is more mobile and, therefore, easier to detect than the herbivorous basal prey, is also quick to escape to hideouts and, therefore, as difficult to catch as the basal prey. Thereafter, we assume that the habitat is open and lacks hideouts, creating a situation where $a_p \ll \alpha$.

When constructing our graphs we assume that $b = 0.9\beta$, i.e. that there is only a 10% difference between the daily energy needs of the two interacting predators. This is an optimistic assumption from the point of view of the top predator. Other parameter values are inferred from the biology of the focal system (see Table 2). Conditions for co-existence will be explored as done by Holt and Polis (1997): by allowing a two-species sub-community to reach its equilibrium and by studying whether the third species could invade this equilibrium.

Table 2. Definitions of model variables and parameters, and their default values

Symbol	Value	Unit	Description
Basal prey			
H	. . .	$ind_H \times ha^{-1}$	Population density
r	varied	day^{-1}	Increase rate
K	varied	$ind_H \times ha^{-1}$	Carrying capacity
Intermediate consumer			
C	. . .	$ind_C \times ha^{-1}$	Population density
b	0.01	$ind_C \times ind_H^{-1}$	Conversion efficiency (basal prey to intermediate consumer)
a_c	0.05	$ha \times day^{-1} \times ind_C^{-1}$	Searching efficiency (for basal prey)
h	0.2	$day \times ind_C \times ind_H^{-1}$	Handling time (of basal prey)
m	0.0082	day^{-1}	Mortality rate
Top predator			
P	. . .	$ind_P \times ha^{-1}$	Population density
β	0.009	$ind_p \times ind_{HorC}^{-1}$	Conversion efficiency (basal prey or intermediate consumer to top predator)
a_p	0.05	$ha \times day^{-1} \times ind_P^{-1}$	Searching efficiency (for basal prey)
η	0.2	$day \times ind_P \times ind_{HorC}^{-1}$	Handling time (of basal prey and intermediate consumer)
α	0.05	$ha \times day^{-1} \times ind_P^{-1}$	Searching efficiency (for intermediate consumer)
μ	0.0082	day^{-1}	Mortality rate

Note: ha = hectare, ind = individual. Parameter values deduced from Ylönen *et al.* (2003).

SUSTENANCE AND INVASION CRITERIA IN THE *r* vs. *K* PARAMETER SPACE

To begin, we will solve the criteria for the ability of the system to sustain the intermediate and top predators in the absence of each other. The sustenance criterion for the intermediate predator (C) is then obtained by setting $H = K$, $P = 0$, and $dC/dt > 0$ in equation (2) and by solving for K, which yields the following condition:

$$K > \frac{m}{a_c(b - hm)} \tag{4}$$

When the basal prey's carrying capacity exceeds this value, the intermediate predator can have a positive rate of population growth. Correspondingly, the sustenance criterion for the top predator (P) in the absence of the intermediate predator is obtained by setting $H = K$, $C = 0$, and $dP/dt > 0$ in equation (3) and by solving for K, which yields the following condition:

$$K > \frac{\mu}{a_p(\beta - \eta\mu)} \tag{5}$$

The invasion criterion for the top predator is found by exploring the conditions under which its *per capita* growth rate is positive when its own density is infinitely low and the community

is at the intermediate predator–basal prey (*C*–*H*) equilibrium, i.e. when $dH/dt = dC/dt = 0$ and $C \approx 0$ in equations (1) and (2). This requires that inequality (6) is satisfied:

$$\frac{\beta(a_p H + \alpha C)}{1 + \eta(a_p H + \alpha C)} > \mu \tag{6}$$

Substituting *H* and *C* with their steady-state values at the *C*–*H* equilibrium (fourth solution from equation A1 in the Appendix) results in the following invasion criterion for the top predator:

$$\frac{a_c K\beta((b - hm)(a_p m + br\alpha)) - mbr\alpha\beta}{a_c K(b - hm)(a_c(b - hm) + \eta(a_p m + br\alpha)) - mbr\alpha\eta} > \mu \tag{7}$$

Conversely, the intermediate predator can invade a community that is at the top predator–basal prey (*P*–*H*) equilibrium if and only if its gain from preying on the basal prey allows for a net reproduction exceeding the mortality resulting from predation by the top predator (i.e. $dC/dt > 0$ when $C \approx 0$ in equation 2). This is done by setting $C = 0$ in equation (2) and exploring the conditions for $dC/dt > 0$. Substituting *P* by its equilibrium value in the absence of *C* (from equation 3), dividing by *H* and rearranging, this criterion results in inequality (8):

$$\frac{ba_c H}{1 + a_c h H} > m + \frac{\alpha P}{1 + a_p \eta H} \tag{8}$$

Substituting *H* and *P* with their steady-state values (fifth solution from equation A1 in the Appendix) gives, finally, the following invasion criterion for the intermediate predator:

$$\frac{a_c b\mu}{a_c h\mu + a_p(\beta - \eta\mu)} > \frac{a_p K(\beta - \eta\mu)(a_p m + r\alpha) - r\alpha\mu}{a_p^2 K(\beta - \eta\mu)} \tag{9}$$

Next, we rearrange inequalities (7) and (9) by solving for *r*. The expressions $b - hm$ and $\beta - \eta\mu$ occur repeatedly in inequalities (7) and (9). These expressions represent the maximum per capita rates of population growth for the intermediate predators and top predators, respectively. Without loss of generality, we can thus define $q = b - hm$, and $\rho = \beta - \eta\mu$. The invasion criterion for the top predator is obtained as follows:

$$r > \frac{a_c Kq(a_c \mu q - a_p m\rho)}{b\alpha\rho(a_c Kq - m)} \tag{10}$$

Correspondingly, the invasion criterion for the intermediate predator is obtained as

$$r < \frac{a_p^2 K\rho(a_p m\rho - a_c \mu q)}{\alpha(a_c h\mu + a_p \rho)(\mu - a_p K\rho)} \tag{11}$$

We see that the denominator of the right-hand side of inequality (10) approaches zero when $K \to m/(a_c q) = m/(a_c(b - hm))$, which is the right-hand side of inequality (4). Thus, the invasion criterion of the top predator has the sustenance criterion of the intermediate predator as its vertical asymptote. A similar exercise with equation (11) reveals that the denominator of its right-hand side approaches zero when $K \to \mu/(a_p \rho)$. That is, the sustenance criterion of the intermediate predator is the vertical asymptote of the top predator's invasion criterion. Because we have assumed that $b < \beta$, the invasion criteria

of the two predators must cross, creating a narrow region of stable co-existence for the interacting predators in the vicinities of the part of the parameter space where r has a very high value, whereas K is close to the sustenance criteria of the two predators (Fig. 1).

The sustenance and invasion criteria described above divide the parameter plane into seven regions. To the left of the intermediate predator's sustenance criterion (dotted vertical line in Fig. 1) there is a region denoted 'H' in Fig. 1, where primary productivity is too low to sustain any predators. Thus, two trophic level dynamics prevail (see Oksanen *et al.*, 1981). Between the persistence criteria of the two predators, we find a region marked 'C' in Fig. 1, where only the intermediate predator can persist. Between the top predator's sustenance criterion and the invasion criterion of the intermediate predator, there is a sickle-shaped region labelled '+C−P' (Fig. 1B) where the top predator could persist in the absence of the intermediate predator, but where the intermediate predator will predictably exclude the top predator. Further to the right, between the two invasion criteria, there is a large region, marked '−C−P' (Figs. 1A and 1B), where the priority effect prevails. At higher r-values, we find a region marked '−C+P' (Figs. 1A and 1C), where the intermediate predator could persist when alone but where the top predator will predictably exclude the intermediate predator. Finally, there are also narrow regions of stable co-existence: the '+C+P' region, where both can co-exist and also persist independently and '+C(+P)', where the top predator is dependent on the intermediate predator (Fig. 1C).

We now move to an open habitat where $a_p \ll \alpha$. Letting $K \to \infty$ in the right-hand side of inequality (10), we obtain the horizontal asymptote of the top predator's invasion criterion as:

$$r = \frac{a_c \mu q - a_p m \rho}{b \alpha \rho} \tag{12}$$

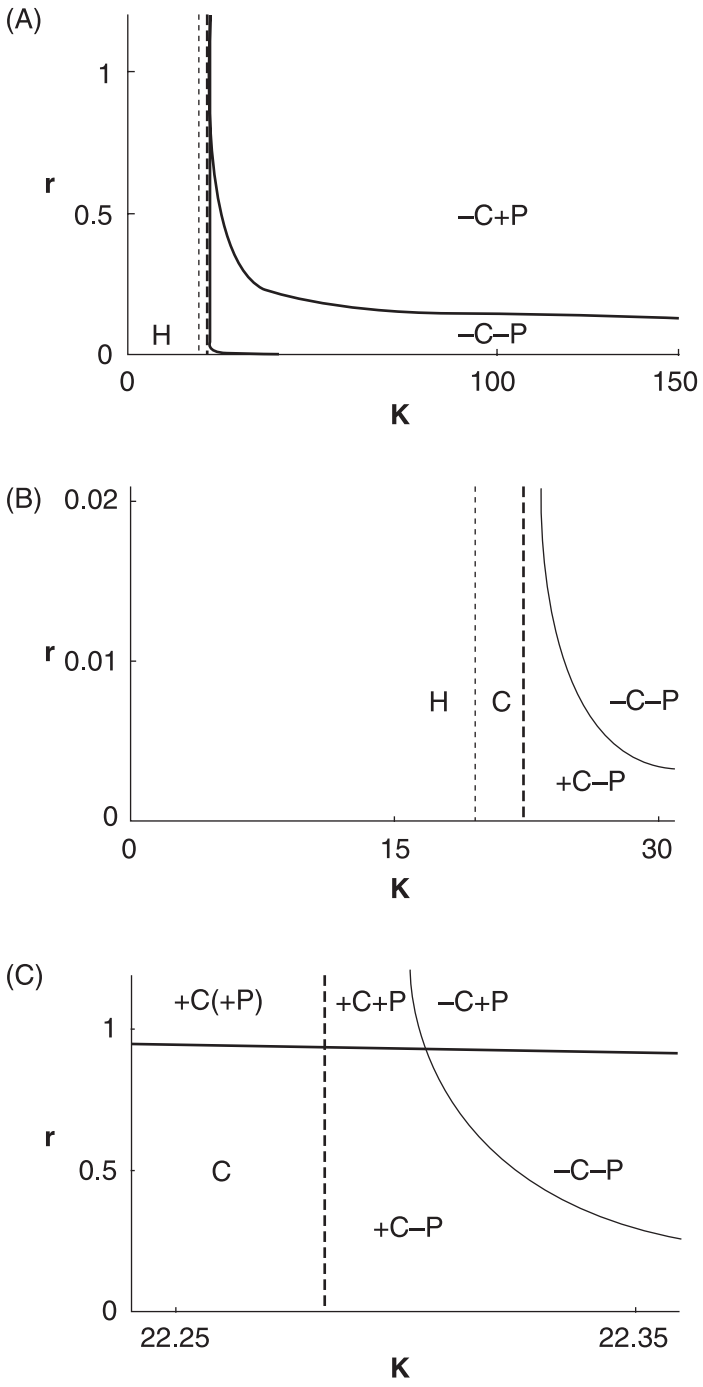
The position of the horizontal asymptote of the top predator's invasion curve thus depends on the ratio of a_c to α. In habitats where intermediate predators are much easier to catch than basal prey, the '−C+P' region descends to low r-values (see Fig. 2, based on the assumption that $\alpha = 5a_p$). Letting $K \to \infty$ in the right-hand side of equation (11), we obtain the horizontal asymptote of the invasion criterion of the intermediate predator as follows:

$$r = \frac{a_c a_p \mu q - a_p^2 m \rho}{\alpha(a_c \alpha h \mu - a_p \rho)} \tag{13}$$

Parameter α appears in the denominator, implying that the position of the horizontal asymptote is inversely proportional to α. Increasing α thus shrinks the '+C−P' area, where the intermediate predator predictably eliminates the top predator (Fig. 2B). Even in such systems, however, the regions of co-existence, '+C+P' and '+C(+P)', are small and restricted to the part of the parameter space where r is very high and K has a low value (Fig. 2C).

IMPACT OF INCREASING PRIMARY PRODUCTIVITY ON GENUINE INTRAGUILD PREDATION SYSTEMS

With increasing primary productivity, the basal prey parameters r and K will increase along the asymptotically rising r vs. K track, which starts from the origin, flattening out when reaching the point ($K = 400$, $r = 0.016$) (see section 'Model structure and parameters'). In


(A)
1
r
0.5
0
H
–C+P
–C–P
0
100
150
K
(B)
0.02
r
0.01
0
H
C
–C–P
+C–P
0
15
30
K
(C)
+C(+P)
+C+P
–C+P
1
r
0.5
0
C
–C–P
+C–P
22.25
22.35
K

habitats where $\alpha = a_p$ (i.e. where intermediate predators are not easier to catch than basal prey; Fig. 1), this track will pass through the regions 'H', 'C', '+C−P', and '−C−P'; i.e. a priority effect is possible but predictable replacement of the intermediate predator by the top predator is not. The horizontal asymptote of the top predator's invasion criterion is $r = 0.15$, which is almost ten times higher then the r_{max} value of *Microtus* voles. As the r_{max} values of all other herbivorous endotherms are still much lower, this result is likely to apply to all endotherm IGP systems.

The priority effect requires that intermediate predator–basal prey equilibrium remains locally stable in highly productive habitats, which is unlikely. Setting $P = 0$ and $dH/dt = 0$ in equation (1) and allowing K to increase *ad infinitum*, we see that with increasing primary productivity, the zero isocline of the basal prey in the intermediate predator–basal prey phase plane (Fig. 3) approaches the line:

$$C = \frac{r_{max}}{a_c} + r_{max}\, hH \tag{14}$$

Thus, there is an upper limit for the response of intermediate predators to increasing primary productivity. Moreover, the basal prey's zero isocline has a positive slope at the basal prey–intermediate predator equilibrium, implying that the system will generate violent limit cycle dynamics (Rosenzweig, 1971). This conclusion also holds for the stacked logistic model (Hanski *et al.*, 1993, 2001; Turchin and Hanski, 1997). In systems exhibiting limit cycle dynamics, increasing primary productivity increases the amplitude of the cycle and *decreases* the minima of the interacting populations, making the invasion of the top predator difficult or impossible (Abrams and Roth, 1994). It is therefore likely that intermediate predators prevail even in highly productive habitats.

In habitats where $a_p \ll \alpha$, the region of priority effect is reached already at moderate values of r and K (see Fig. 2) and, in highly productive habitats, the r vs. K track crosses the invasion criterion of top predators and enters the '−C+P' region. Under this premise, high primary productivity thus leads to predictable exclusion of the intermediate predator.

Fig. 1. Bifurcation plot of the invasibility criteria for the intermediate predator (C) and the top predator (P) in the parameter space defined by the basal prey's carrying capacity (K) and maximal per capita rate of population growth (r), assuming that the top predator has the same searching efficiency for the basal prey and the intermediate predator. Panel (A) provides an overall picture; panels (B) and (C) are enlargements of those parts of the parameter space where panel (A) is not legible due to dense packing of bifurcation lines. The area denoted by 'H' represents parameter values where only the basal prey can persist. The area denoted by 'C' represents parameter values where the intermediate predator can persist but the top predator cannot. In the '+C−P' area, both predators could persist in the absence of each other; the intermediate predator could invade a system with the top predator co-existing with the basal prey but the converse invasion is not possible. In the '−C−P' area, a priority effect prevails. Both predators could persist in the absence of the other, but neither could invade a system where the other has become established. In the '−C+P' area, the top predator could invade a system with basal prey and intermediate predators, driving the intermediate predator to extinction. In the +C+P area, both predators could persist regardless of the presence of the other. In the +C(+P) area, the intermediate predator could persist by exploiting the basal prey, whereas the persistence of the top predator requires the presence of the intermediate predator.

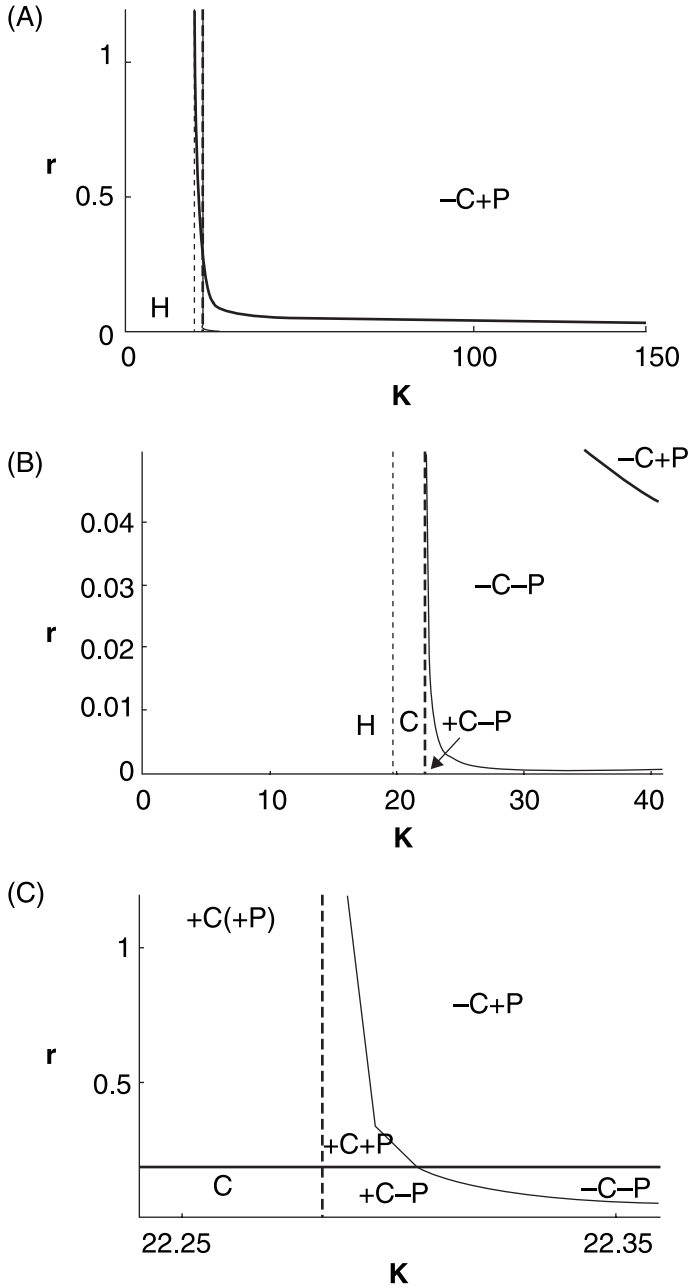


Fig. 2. Bifurcation plot of the invasibility criteria for the intermediate predator (C) and the top predator (P) in the parameter space defined by the basal prey's carrying capacity (K) and maximal per capita rate of population growth (r) assuming that the top predator has five times higher searching efficiency for the intermediate predator than for the basal prey ($\alpha = 5a_p$). Panel (A) provides an overall picture; panels (B) and (C) are enlargements of those parts of the parameter space where panel (A) is not legible due to dense packing of bifurcation lines. Notation as in Fig. 1.

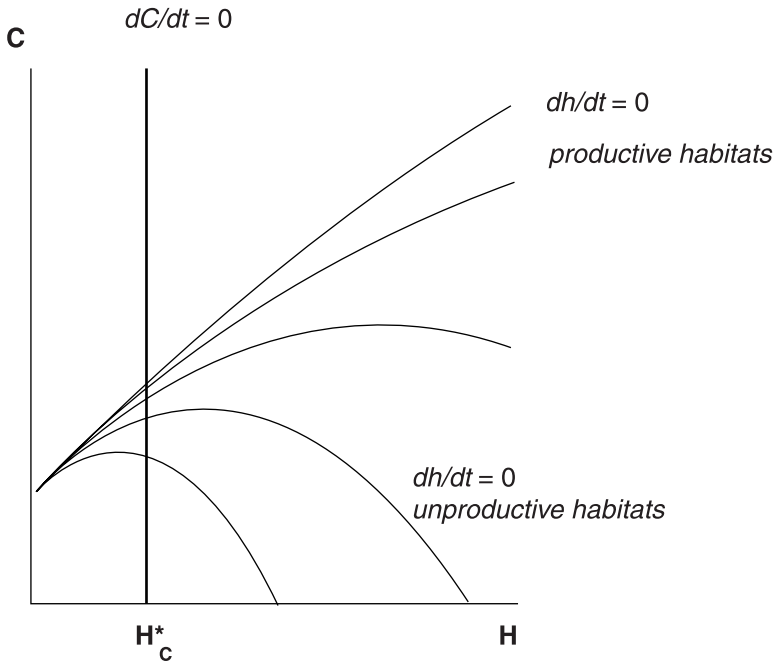


Fig. 3. Phase plane plot of the intermediate predator (C)–basal prey (H) system, illustrating the impact of enrichment on the equilibrium density of the intermediate predator. The parabolas represent the zero isoclines of the basal prey in environments with different levels of enrichment. The vertical line is the zero isocline of the intermediate predator. The intersections represent the equilibrium constellations. Note the marginal effect of high levels of enrichment for the location of the equilibrium point.

DISCUSSION

According to our analysis, predatory interactions between members of the same endotherm guild (Roth, 1967) do not provide a plausible mechanism for interspecific co-existence. The region of stable co-existence is confined to a biologically implausible part of the parameter space, where the basal prey has low K but the prey can nevertheless double its numbers in a single day. Co-existence in intraguild predator (IGP) systems emerges from the ability of the basal prey to support such densities of intermediate predators that they constitute a major resource for the top predators. The discrepancy between the densities of least weasels (2–13 per km^2) and voles (70–2300 per km^2) on the agricultural plains of western Finland (Table 1) illustrates that this mechanism does not work in endotherm IGP systems. In these systems, intraguild predation amounts primarily to an extreme form of interference competition, which does not lead to co-existence (Amarasekare, 2002).

Contrary to the results obtained from food chain omnivory (FCO) systems (Diehl and Feißel, 2000; Mylius *et al.*, 2001; HilleRisLambers and Diekemann, 2003; Snyder *et al.*, 2005), intermediate predators were predicted to prevail even in productive habitats, provided that intermediate predators and basal prey are equally easy to catch. In open habitats, where intermediate predators are exposed and easy to catch, moderate primary productivity leads to a priority effect, and high productivity to predictable replacement of intermediate predators by top predators.

These predictions do not contradict the results deduced from generalized FCO models but do indicate the utility of nuanced terminology. If all kinds of food web omnivory are pooled under a single label, it is difficult to see the consequences of convergent and divergent foraging tactics for stability and co-existence. The proposed terminology helps to see the difference. In IGP systems as defined by us, the order in which the two predators arrive often settles the outcome. If the intermediate predator arrives first, the top predator is forced to interact with a superior resource competitor, whose own contribution to the resource basis of the top predator is negligible. If, in turn, the top predator has become established first, the intermediate predator is exposed to apparent competition (Holt, 1977) with its own prey, which is likely to have higher reproductive capacity and, hence, also a higher *r*/*a* ratio. Therefore, IGP interactions as defined by us are destabilizing. If predators nevertheless co-exist, they do so in spite of intraguild predation, not because of it. If feeding tactics diverge, as they do in systems for which we regard food chain omnivory as the appropriate label, co-existence between intermediate and top predators is possible (Diehl and Feißel, 2000; Mylius *et al.*, 2001; Borer *et al.*, 2003; Takimoto *et al.*, 2007), and in the right dose food chain omnivory might even enhance stability (McCann and Hastings, 1997).

Our analysis refers to dynamics within an infinitely large and homogeneous area, where the only biologically significant interactions are between the three populations modelled. A system approximately conforming to this scenario is formed by arctic foxes (*Alopex lagopus*) and red foxes (*Vulpes vulpes*), exploiting arvicoline rodents in the Fennoscandian inland tundra (Elmhagen *et al.*, 2002). In the past, arctic foxes abounded, and red foxes were confined to boreal forests. After decades of reckless hunting and trapping, arctic foxes became decimated and red foxes invaded the tundra. Arctic foxes have finally become protected, but they have nevertheless continued to decline. Red foxes prey on arctic foxes (Tannerfeldt *et al.*, 2002; Pamperin *et al.*, 2006) and exclude them from their dens (Tannerfeldt *et al.*, 2002). A priority effect, generated by intraguild predation in a habitat where an arctic fox is much easier to find and to catch than a rodent, provides a plausible explanation for the observed dynamics.

In systems of the kind discussed above, intraguild predation is a transient phenomenon, but if each predator has exclusive resources, systems with frequent intraguild predation can persist (Holt and Huxel, 2007; for empirical cases, see Korpimäki and Norrdahl, 1989; Polis *et al.*, 1989, Polis, 1991; Hakkarainen and Korpimäki, 1996; Polis and Strong, 1996; Maran *et al.*, 1998; Palomares and Caro, 1999; Sunde *et al.*, 1999; Fedriani *et al.*, 2000; Gerber and Echternacht, 2000; Arim and Marquet, 2004; Donaldio and Buskirk, 2006; Sergio and Hiraldo, 2008). An example is provided by the North Fennoscandian taiga, which harbours several small and medium sized predators, and all larger species prey on their smaller competitors (Mikkola, 1983; Korpimäki and Norrdahl, 1989; Lindström *et al.*, 1995; Hakkarainen and Korpimäki, 1996; Kurki *et al.*, 1998; Hoset *et al.*, 2009). All predators prefer voles in high-density years but, except for the least weasel (Korpimäki *et al.*, 1991), they also have other options. Predatory birds leave the area in times of vole shortage. Stoats switch to water voles (*Arvicola terrestris*), lagomorphs, gallinaceous birds, and other avian prey (Myrberget, 1975; Danilov and Tumanov, 1976; Korpimäki *et al.*, 1991; Aunapuu and Oksanen, 2003). Pine martens (*Martes martes*) switch to red squirrels (*Sciurus vulgaris*) (Pulliainen and Ollimäki 1996). Red foxes cope with a shortage of voles by using larger prey (Dell'Arte *et al.*, 2007) and frozen carrion (Helldin and Danielsson, 2007). Each competing species has a lowest R^* value for some resource type, which allows for competitive co-existence (MacArthur, 1972; Tilman, 1982).

Exclusive resources, supporting bigger predators, can, however, raise the IGP pressure experienced by the smallest predator to a fatally high level (Holt and Huxel, 2007). This probably

happened in northern Fennoscandia during the 1980s, when the alien American mink became established. The least weasel became marginalized and multi-annual vole cycles were replaced by primarily seasonal density variations (Hanski and Henttonen, 1996; Oksanen and Henttonen, 1996; Ekerholm *et al.*, 2001), leading to the decline of northern raptor populations (Kjellén and Roos, 2000). It is unlikely that mink densities had been high enough to have much direct impact on vole dynamics. However, the mink uses aquatic prey (i.e. has an exclusive resource that native predators cannot exploit) and preys efficiently upon all smaller animals (Banks *et al.*, 2008). Mink also shares the habitat preferences of the least weasel (Oksanen *et al.*, 1992; Aunapuu and Oksanen, 2003). The IGP impact of the mink probably changed the outcome of the stoat–weasel–vole interaction to the favour of the stoat, which is less likely to drive multi-annual vole cycles (Hanski and Henttonen, 1996; Oksanen *et al.*, 2001).

Systems with intraguild predation should also be sensitive to small differences in external conditions, if these influence the searching efficiency of larger predators on their smaller competitors. A possible example is provided by the predator communities and predator–prey dynamics on the agricultural plains of southern Sweden and western Finland. Both areas have thin snow cover (average annual maximum < 30 cm), but its average duration in western Finland is about 3–4 months as opposed to less than one month in southern Sweden (http://www.fmi.fi/saa/tilastot_10.html and http://www.his.se/PageFiles/2930/sveriges_klimat_07.ppt?epslanguage=sv#298,22,Antal dygn med snötäcke/år). Both areas are productive and harbour high densities of predatory birds and mammals (Erlinge *et al.*, 1983; Korpimäki and Norrdahl, 1991), but in different abundance relationships. Vole dynamics are also different. In western Finland, vole populations (*Microtus* spp. and *Myodes glareolus*) display 3-year high-amplitude multi-annual cycles, which are synchronous over distances up to 600 km (Korpimäki *et al.*, 2005a, 2005b). The most abundant predator of voles is the least weasel (Table 1), which is also the most common cause of vole mortality (Norrdahl and Korpimäki, 1995a). Intraguild predation is common, especially in the decline phase of the vole cycle (Korpimäki and Norrdahl, 1989; Dell'Arte *et al.*, 2007); it resulted in an approximately 80% loss of least weasels in 1984 and 1987 (Korpimäki and Norrdahl, 1989). Nevertheless, least weasels dominate numerically and, together with avian predators, drive the vole cycles of the area (Korpimäki and Norrdahl, 1998; Korpimäki *et al.*, 2002; see also Norrdahl and Korpimäki, 1995b).

In southern Sweden, vole populations fluctuate seasonally. The predator guild is dominated by medium-sized mammalian and avian predators (Erlinge *et al.*, 1983). The difference between the two areas has been explained as a consequence of better availability of alternative prey, primarily rabbits (*Oryctolagus cuniculus*), in southern Sweden (Erlinge *et al.*, 1983) and the consequent prevalence of generalists with a stabilizing functional response (Andersson and Erlinge, 1977; Hanski *et al.*, 1991). [The lagomorphs of western Finland are too large to play a similar role (see Korpimäki and Norrdahl, 1991; Korpimäki *et al.*, 1991; Norrdahl and Korpimäki, 1995c), and the subterranean water voles, *Arvicola terrestris*, are well protected (see Korpimäki *et al.*, 2005a).] However, there is little evidence for the conjecture of stabilizing functional response in the medium-sized predators of temperate Europe (Oksanen *et al.*, 2001; Korpimäki *et al.*, 2005b). A difference in the duration of the snowy periods between the two areas and the consequent difference in the exposure of the smallest predators to intraguild predation provides an alternative explanation. Due to higher exposure to intraguild predation, the small mammalian predators of southern Sweden are confined to especially protected habitats, such as vicinities of stone fences (Erlinge, 1974, 1977; Erlinge and Sandell, 1988). In western Finland, the longer snowy periods provide least weasels enough protection to switch the balance in its favour (Amarasekare, 2008; see also Korpimäki *et al.*, 1991). The larger predators survive

because of their mobility (birds) or because of access to alternative prey (Korpimäki and Norrdahl, 1991; Korpimäki *et al.*, 1991).

Intraguild predation can thus have major impacts on abundance relationships and the habitat use of predators, and it can amplify the impacts caused by direct human interferences and by invasions of alien predators. Within each habitat, intraguild predation tends to result in elimination of one of the interacting species, as predicted by Pimm and Lawton (1978), but exclusive resources (Holt and Huxel, 2007) and spatial heterogeneity (Snyder *et al.*, 2005) allow co-existence, at least on the landscape level, creating a situation where intraguild predation can frequently occur in spite of its destabilizing potential.

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APPENDIX

Steady-state points of the system described by equations (1)–(3)

$$\begin{Bmatrix} H \to 0 & C \to 0 & P \to 0 \\ H \to 0 & C \to 0 & P \to 0 \\ H \to K & C \to 0 & P \to 0 \\ H \to \dfrac{m}{a_c\,(b - hm)} & C \to \dfrac{br\,(a_c K\,(b - hm) - m)}{a_c^2 K (b - hm)^2} & P \to 0 \\ H \to \dfrac{\mu}{a_p\,(\beta - \eta\mu)} & C \to 0 & P \to \dfrac{\beta r\,(a_p K\,(\beta - \eta\mu) - \mu)}{a_p^2 K\,(\beta - \eta\mu)^2} \\ H \to x & C \to y & P \to z \end{Bmatrix}$$

where

$$x = -\frac{1}{2hr\alpha\,(\beta - \eta\mu)\,a_c}$$
$$\Big(r\alpha\beta - r\alpha\eta\mu - hKr\alpha\beta a_c + hKr\alpha\eta\mu a_c - K\beta a_c a_p + bK\beta^2 a_c a_p - hKm\beta^2 a_c a_p +$$
$$K\eta\mu a_c a_p - bK\beta\eta\mu a_c a_p + hKm\beta\eta\mu a_c a_p +$$
$$\sqrt{\Big((\beta - \eta\mu)\,\big(-4\,hKr\alpha a_c\,(\mu a_c - (\beta - \eta\mu)\,(r\alpha + m\beta a_p)) +$$
$$(\beta - \eta\mu)\,(r\alpha - Ka_c\,(hr\alpha + (1 - b\beta + hm\beta)\,a_p))^2\big)\Big)};$$

$$y = \frac{1}{2hr\alpha^2\,(\beta - \eta\mu)\,a_c}$$
$$\Big(a_c\,(2hr\alpha\mu + K\,(\beta - \eta\mu)\,a_p\,(-hr\alpha + (-1 + b\beta - hm\beta)\,a_p)) +$$
$$a_p$$
$$\Big(r\alpha\,(\beta - \eta\mu) +$$
$$\sqrt{\Big((\beta - \eta\mu)\,\big(r^2\alpha^2\,(\beta - \eta\mu) + Ka_c\,(2r\alpha\,(\beta - \eta\mu)\,(hr\alpha + (-1 + b\beta + hm\beta)\,a_p) +$$
$$a_c\,(hr\alpha\,(-4\mu + hKr\alpha\,(\beta - \eta\mu)) + K\,(1 - b\beta + hm\beta)\,(\beta - \eta\mu)\,a_p$$
$$(2hr\alpha + (1 - b\beta + hm\beta)\,a_p))))\Big)\Big)\Big)\Big)\Big)};$$

$$z =$$
$$\Big(\beta$$
$$\Big((b + hm)\,r\alpha\,(-\beta + \eta\mu) +$$
$$(-b + hm)\,\big(K\,(\beta - \eta\mu)\,a_c\,(-hr\alpha + (-1 + b\beta - hm\beta)\,a_p) +$$
$$\sqrt{\Big((\beta - \eta\mu)\,\big(r^2\alpha^2\,(\beta - \eta\mu) + Ka_c\,(2r\alpha\,(\beta - \eta\mu)\,(hr\alpha + (-1 + b\beta + hm\beta)\,a_p) +$$
$$a_c\,(hr\alpha\,(-4\mu + hKr\alpha\,(\beta - \eta\mu)) + K\,(1 - b\beta + hm\beta)\,(\beta - \eta\mu)\,a_p$$
$$(2hr\alpha + (1 - b\beta + hm\beta)\,a_p))))\Big)\Big)\Big)\Big)\Big)\Big)/$$
$$\Big(h\alpha\,(\beta - \eta\mu)\,\big(r\alpha\,(\beta - \eta\mu)\,(1 + hKa_c) - K\,(-1 + b\beta - hm\beta)\,(\beta - \eta\mu)\,a_c a_p -$$
$$\sqrt{\Big((\beta - \eta\mu)\,\big(-4\,hKr\alpha a_c\,(\mu a_c - (\beta - \eta\mu)\,(r\alpha + m\beta a_p)) +$$
$$(\beta - \eta\mu)\,(r\alpha - Ka_c\,(hr\alpha + (1 - b\beta + hm\beta)\,a_p))^2\big)\Big)\Big)\Big).$$