

## THE INTERACTION OF CANNIBALISM AND OMNIVORY: CONSEQUENCES FOR COMMUNITY DYNAMICS

VOLKER H. W. RUDOLF<sup>1</sup>

*Department of Biology, University of Virginia, Charlottesville, Virginia 22904 USA*

**Abstract.** Although cannibalism is ubiquitous in food webs and frequent in systems where a predator and its prey also share a common resource (intraguild predation, IGP), its impacts on species interactions and the dynamics and structure of communities are still poorly understood. In addition, the few existing studies on cannibalism have generally focused on cannibalism in the top-predator, ignoring that it is frequent at intermediate trophic levels. A set of structured models shows that cannibalism can completely alter the dynamics and structure of three-species IGP systems depending on the trophic position where cannibalism occurs. Contrary to the expectations of simple models, the IG predator can exploit the resources more efficiently when it is cannibalistic, enabling the predator to persist at lower resource densities than the IG prey. Cannibalism in the IG predator can also alter the effect of enrichment, preventing predator-mediated extinction of the IG prey at high productivities predicted by simple models. Cannibalism in the IG prey can reverse the effect of top-down cascades, leading to an increase in the resource with decreasing IG predator density. These predictions are consistent with current data. Overall, cannibalism promotes the coexistence of the IG predator and IG prey. These results indicate that including cannibalism in current models can overcome the discrepancy between theory and empirical data. Thus, we need to measure and account for cannibalistic interactions to reliably predict the structure and dynamics of communities.

**Key words:** *cannibalism; community structure and dynamics; competition; effect of enrichment; food web; intraguild predation; intraspecific predation; predator–prey interactions; size structure.*

### INTRODUCTION

One of the simplest forms of omnivory is intraguild predation (IGP), where an omnivorous predator competes with its prey for a shared resource. Based on the seminal theory developed by Holt and Polis (1997) and subsequent extensions of this model (Diehl and Feissel 2000, Mylius et al. 2001, Diehl 2003, Tanabe and Namba 2005), it is generally believed that coexistence of the IG predator and the IG prey is only possible under very limited conditions, and only if the prey is more efficient in resource exploitation. These predictions corroborate with the previous opinion that omnivory can be destabilizing compared to simple linear food chains (Pimm and Lawton 1978). Although there is some empirical support for these predictions in microbial systems (Morin 1999, Diehl and Feissel 2000, 2001), this commonly conflicts with the empirical data and recent meta-analyses that show intraguild predation is a common and stable form of species interaction (Polis et al. 1989, Fagan 1997, Holyoak and Sachdev 1998, Arim and Marquet 2004). Furthermore, field experi-

ments have not consistently shown that the IG predator is less efficient in resource exploitation (Vance-Chalcraft et al. 2007). This poses the question of whether we are missing some crucial part of reality in current models.

Previous models have focused on homogeneous populations without size structure (but see Mylius et al. 2001), and generally ignored size-specific interactions within a species. Most organisms, however, undergo considerable changes in size during their ontogeny and different sized cohorts commonly coexist (Polis 1984). As a consequence, cannibalism and asymmetrical competitive and behavioral interactions are a prevalent feature in such size-structured populations and communities (Sih 1981, Persson et al. 2000, Rudolf 2006). Recent empirical and theoretical work has shown that cannibalistic interactions can have important consequences for species interactions and the structure of whole communities and can result in dynamics that are not predictable from unstructured systems (Sih 1981, Persson et al. 2000, 2003, Claessen et al. 2004, Rudolf 2006, 2007). The reason for these dynamical differences is that cannibalism introduces a trophic structure within the population that allows for indirect interactions even in simple two species systems (Rudolf 2006). Cannibalism is ubiquitous in aquatic and terrestrial food webs (Fox 1975, Polis et al. 1989) and it is increasingly recognized that cannibalism is present in the majority of IGP systems (Polis et al. 1989, Woodward and Hildrew 2002). However, no detailed theoretical study has

Manuscript received 25 July 2006; revised 16 October 2006; accepted 14 November 2006. Corresponding Editor (ad hoc): J. A. Rosenheim. For reprints of this Special Feature, see footnote 1, p. 2679.

<sup>1</sup> Present address: Department of Ecology and Evolutionary Biology, Rice University, 6100 Main St., Houston, Texas 77005 USA. E-mail: volker.rudolf@rice.edu

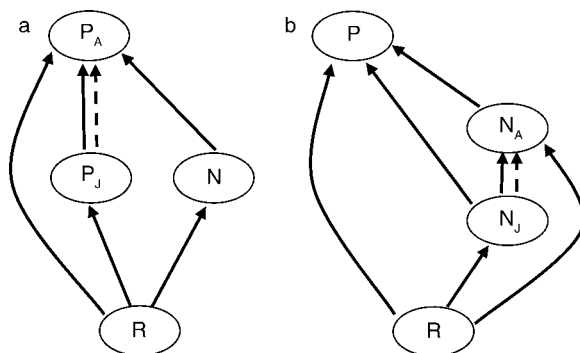


FIG. 1. Different food web topologies of intraguild predation (IGP) systems analyzed in this study with (a) cannibalism in the stage-structured predator (P), and (b) cannibalism in the stage-structured prey (N). Cannibalistic interactions are size- or stage-structured, where large adults (subscript A) consume smaller juvenile conspecifics (subscript J). Both predator and prey compete for the common resource, R. Solid arrows indicate feeding relationships from resource to consumer; dashed arrows indicate growth transitions.

examined the effect of size-structured cannibalism on the dynamics of IGP systems. Furthermore, although cannibalism is frequent in top predators, previous studies have largely overlooked its common occurrence in a variety of functional groups and trophic levels, including intermediate predators, but also many so-called herbivores and detritivores (Fox 1975).

Current theory regarding intraguild predation makes four major predictions (Holt and Polis 1997): (1) for both the IG prey and predator to coexist, the prey has to be more efficient in exploiting the common resource and the predator has to gain significantly from consuming the IG prey, (2) the IG prey will invade a system at lower productivity of the bottom resource, and with sufficiently high enrichment of the system the prey will ultimately be driven to extinction by the predator via apparent competition, and (3) decreasing the density of the predator will decrease the bottom resource, (4) coexistence of the predator and prey is only possible for a very small region of the parameter space. In this study, I develop models that include stage-structured cannibalism at different trophic levels (i.e., in the IG predator or prey) to examine how cannibalism alters the dynamics of IGP systems. In particular, I examine how cannibalism alters the coexistence conditions with respect to the relative competitiveness of IG prey and predator, the conditions for invasion, the effect of enrichment, and how changing the predator density affects the bottom resource. Results show that cannibalism can result in patterns that are consistent with empirical data but cannot be predicted with classical IGP theory.

#### THE BASIC MODELS

Here, I examine two basic IGP systems with cannibalism in (1) the IG predator and (2) the IG prey

(Fig. 1a, b). The basic model is based on the classical system first introduced by Holt and Polis (1997) consisting of a common resource R, the IG prey N, and the IG predator P. To allow for the naturally size-structured and asymmetric interaction between cannibals and conspecific prey observed in empirical systems, the cannibalistic species is separated into two stages: a cannibalistic adult stage ( $X_A$ ) and a non-cannibalistic juvenile stage ( $X_J$ ).

#### Cannibalism in the IG predator

In this scenario (Fig. 1a), adult IG predators ( $P_A$ ) consume the IG prey, N, and both adult and juvenile predators ( $P_J$ ) and the prey consume the common resource, R. Thus, this scenario represents an increase in the diet breadth of the predator with increasing size/age which is characteristic for many predatory species (Polis 1984). A general description of the parameters and variables is given in Table 1. The dynamics of such a system are given by

$$\frac{dR}{dt} = R[r(R) - a(R, N, P)N - \alpha(R, N, P)P_A - \alpha(R, N, P)P_J] \quad (1a)$$

$$\frac{dN}{dt} = N[e_{RN}a(R, N, P)R - h(R, N, P)P_A - \mu_N] \quad (1b)$$

$$\frac{dP_J}{dt} = P_A[e_{RP}\alpha(R, N, P)R + e_{NP}h(R, N, P)N + (e_P - 1)\beta(R, N, P)P_J] - (m + \mu_J)P_J \quad (1c)$$

$$\frac{dP_A}{dt} = mP_J - \mu_A P_A \quad (1d)$$

where R, N,  $P_J$ , and  $P_A$  are the densities of the resource, the IG prey, and the juvenile and adult IG predator, respectively.

If only juveniles, not adults, are consuming the resource [i.e.,  $\alpha(R, N, P) = 0$ ], the system folds back into a simple food chain in which the IG predator could not persist without the IG prey, N. If juveniles would also be able to consume the IG prey, this would have a general negative effect on invasion and persistence of the IG prey and reduce the range of coexistence of both IG predator and IG prey without cannibalism. The model assumes no reproduction in the juvenile predator stage since this is the most common scenario in nature. Furthermore, this also represents the best-case scenario for the prey to persist at higher resource levels.

#### Cannibalism in the IG prey

Similarly, cannibalism is introduced in the IG prey by separating the consumer N into a cannibalistic adult stage ( $N_A$ ) and non-cannibalistic juvenile stages ( $N_J$ ), which are both subject to predation by the IG predator P. Both prey stages and the predator consume the common resource R. The dynamics of the system are

TABLE 1. Definitions of model parameters.

Parameter	Definition
Population state variables	
$R$	Density of shared bottom resource
$N_A, N_J$	Density of adult prey (cannibals) and juvenile prey (N)
$P_A, P_J$	Density of adult (cannibals) and juvenile predators (P)
Growth and feeding	
$r(R)$	Growth rate of resource
$a(R, N, P), a'(R, N, P)$	Functional response of prey, unstructured/adult and juvenile stage
$\alpha(R, N, P), \alpha'(R, N, P)$	Functional response of predator, unstructured/adult and juvenile stage, with respect to the resource (R)
$h(R, N, P), h'(R, N, P)$	Functional response of predators with respect to prey (N)
$\beta(R, N, P)$	Cannibalistic predation rate
Other parameters	
$m$	Density-independent maturation rate coefficient
$\mu_A, \mu_J$	Density-independent mortality rate of adults and juveniles
$\mu_N, \mu_P$	Density-independent mortality rate of unstructured prey and predator
$e_{RN}, e_{RNA}, e_{RNJ}$	Resource conversion efficiency of prey, adults and juveniles
$e_{RP}, e_{RPA}, e_{RPJ}$	Resource conversion efficiency of predator, adults and juveniles
$e_{NP}, e_{NAP}, e_{NJP}$	IG prey (adults and juveniles) conversion efficiency of predator
$e_N, e_P$	Cannibalism conversion coefficient of prey and predator
$K$	Carrying capacity of the resource

given by

$$\frac{dR}{dt} = R[r(R) - a(R, N, P)N_A - a'(R, N, P)N_J - \alpha(R, N, P)P] \tag{2a}$$

$$\frac{dN_J}{dt} = N_A[e_{RNA}a(R, N, P)R + (e_N - 1)\beta(R, N, P)N_J] - [h'(R, N, P)P + m + \mu_J]N_J \tag{2b}$$

$$\frac{dN_A}{dt} = mN_J - N_A[h(R, N, P)P + \mu_A] \tag{2c}$$

$$\frac{dP}{dt} = P[e_{RP}\alpha(R, N, P)R + e_{NAP}h(R, N, P)N_A + e_{NJP}h'(R, N, P)N_J - \mu_P] \tag{2d}$$

where  $R, N_J, N_A,$  and  $P$  are the densities of the resource, the juvenile and adult IG prey, and the IG predator, respectively. As in the previous case, only the cannibalistic stage is reproductive. Although this is the more common form in natural systems (because cannibalism is generally a size-structure interaction and reproductive individuals are usually similar in size in species with determinant growth), note that this formulation favors the predator because competition between the two prey stages reduces the equilibrium densities of the prey.

RELATIVE COMPETITIVENESS IF IG PREY AND PREDATOR

In simple IGP systems, the relative efficiencies of resource exploitation by the IG prey and the predator have important consequences for the coexistence of both IG predator and prey. The general effect of cannibalism on this condition can be examined by focusing on the

dynamic equations of the predator and prey at the three-species equilibrium ( $R^*, N^*, P^*$ ) (Holt and Polis 1997). The dynamic equations of the IG prey (Eq. 1b) and the predator (Eq. 1c) can be separated into two and three major terms, respectively: A general per capita growth rate of the predator,  $f_P(R^*)$ , and the prey,  $f_N(R^*)$ , as a function of the resource density at equilibrium ( $R^*$ ), and the respective per capita mortality rate ( $h(R^*, N^*, P^*)P_A^*$ ) and the increase in reproductive output due to intraguild predation ( $e_{NP}h(R^*, N^*, P^*)N^*$ ) or cannibalism ( $(1 - e_P)\beta(R^*, N^*, P^*)P_A^*\mu_A/m$ ).

In the first scenario with cannibalism in the predator, it follows from Eqs. 1a–d that at the stable three-species equilibrium, assuming one exists, it is necessary that

$$f_N(R^*) = h(R^*, N^*, P^*)P_A^* \tag{3a}$$

$$f_P(R^*) = -e_{NP}h(R^*, N^*, P^*)N^* + (1 - e_P)\beta(R^*, N^*, P^*)\lambda P_A^* \tag{3b}$$

with  $\lambda = \mu_A/m$  and  $P_J^* = \lambda P_A^*$ . Without cannibalism (i.e.,  $\beta = 0$ ), it follows that  $f_P(R^*) < 0 < f_N(R^*)$ . In other words, the IG prey has to be superior in exploiting the resource relative to the IG predator for all three species to coexist. However, with cannibalism (i.e.,  $\beta > 0$ ) the prey, N, can invade the P, R system and coexist with the predator if

$$f_N(R^*) + \frac{e_{NP}h(R^*, N^*, P^*)f_P(R^*)}{(e_P - 1)\beta(R^*, N^*, P^*)\lambda} > 0. \tag{4}$$

This implies that with cannibalism in the IG predator, both predator and prey can coexist even if the predator is superior in exploiting the resource [i.e.,  $f_P(R^*) > f_N(R^*)$ ], as long as the mortality imposed on the prey by

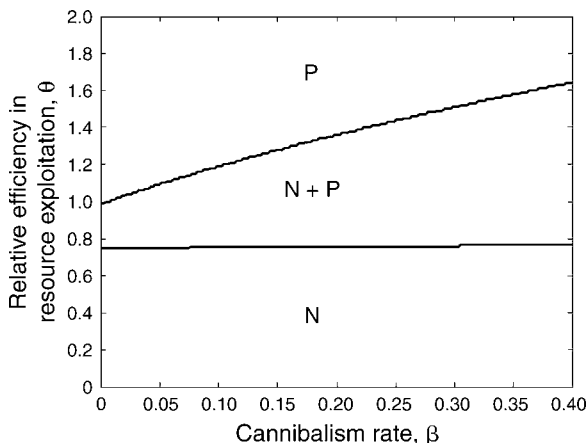


FIG. 2. Effect of cannibalism by the predator on the outcome of resource competition between predator (P) and prey (N) on the regions of three possible equilibria conditions of both species. For each region the steady states are indicated: N, prey equilibrium; P, predator equilibrium; N + P, prey–predator equilibrium. The relative efficiency in resource exploitation  $\theta = e_{RNA}/e_{RN}\alpha$ ;  $r = 0.4$ ,  $\beta_{RP} = 0.2$ ,  $h = 0.5$ ,  $e_{NP} = 0.5$ ;  $e_P = 0.5$ ;  $m = 0.1$ ;  $\mu_C = \mu_{PA} = \mu_{PJ} = 0.06$ ,  $\alpha = \alpha'$ . Parameters are defined in Table 1.

the predator is smaller than the mortality of the predator due to cannibalism [i.e.,  $h(R^*, N^*, P^*) < (e_P - 1)\beta(R^*, N^*, P^*)\lambda$ ] (Fig. 2). Note that this is consistent with simpler unstructured models with density-dependent mortality (Polis et al. 1989). The more cannibalistic the IG predator is (larger  $\beta$ ), the more efficient it can be in exploiting the resource relative to the prey without excluding the prey (Fig. 2). If juveniles are also preying on the IG prey, cannibalism has to be even higher to compensate for the additional mortality in the IG prey.

A similar analysis for the second scenario with cannibalism in the prey (Eqs. 2a–d) reveals that cannibalism does not alter the general condition for coexistence. In this scenario, the prey still has to exploit the resource more efficiently [i.e.,  $f_P(R^*) < 0 < f_N(R^*)$ ] for both prey and predator to coexist.

INVASION, EXTINCTION, AND THE EFFECT OF ENRICHMENT

For the sake of simplicity, and to allow for a direct comparison to previous classical IGP models, assume a linear Lotka-Volterra type functional response, with logistic growth in the resource to examine the effect of enrichment on the conditions of coexistence. In particular, let  $a(R, C, P) = a$ ,  $a'(R, N, P) = a'$ ,  $\alpha(R, N, P) = \alpha$ ,  $\alpha'(R, N, P) = \alpha'$ ,  $\beta(R, N, P) = \beta$ ,  $h(R, N, P) = h$ ,  $h'(R, N, P) = h'$ , and  $r(R) = r(1 - R/K)$ .

Cannibalism in the predator

The dynamics of the system with linear functional responses are given by

$$\frac{dR}{dt} = R \left[ r \left( 1 - \frac{R}{K} \right) - aN - \alpha P_A - \alpha' P_J \right] \tag{5a}$$

$$\frac{dN}{dt} = N(e_{RNA}aR - hP_A - \mu_N) \tag{5b}$$

$$\frac{dP_J}{dt} = P_A [e_{RP}\alpha R + e_{NP}hN + (e_P - 1)\beta P_J] - (m + \mu_J)P_J \tag{5c}$$

$$\frac{dP_A}{dt} = mP_J - \mu_A P_A. \tag{5d}$$

Cannibalism never influences the invasion of the cannibalistic species itself (Rudolf 2007). This makes intuitive sense because the density of the species will be negligibly small during the initial stage of invasion, and thus the probability of mortality due to cannibalistic encounters is negligible. The Appendix shows that the IG predator can invade into the N and R system if  $e_{RP}\alpha\mu_N/e_{RNA} + e_{NP}h(1 - \mu_N/e_{RNA}aK)r/a - \mu_A - \mu_J\lambda > 0$ . Thus, enrichment of the system (i.e., increase in  $K$  or  $r$ ) will reduce the invasion threshold and facilitate the invasion of the predator when the  $R^* - N^*$  system is at equilibrium (Fig. 3a).

Unlike for the predator, the invasion condition for the IG prey (N) is strongly altered by cannibalism in the predator. In general terms, the prey can invade the R and P system if

$$e_{RNA}R^* - (hP_A^* - \mu_N) > 0. \tag{6}$$

In other words, the reproductive output of the prey has to be larger than its total mortality. The effect of cannibalism on this condition depends on how the resource density changes relative to the IG predator's density with changes in the cannibalism rate (i.e., on  $dR^*/d\beta$  vs.  $dP_A^*/d\beta$ ). The Appendix shows that with a linear functional response of the predator the resource will always increase with an increase in cannibalism (i.e.,  $dR^*/d\beta > 0$ ), while the predator always decreases ( $dP_A^*/d\beta < 0$ ). Thus, cannibalism will facilitate the invasion of the IG prey and increase the region of coexistence of the IG predator and prey (Fig. 2). With a nonlinear functional response (i.e., Holling type II) the density of the predator can increase with higher cannibalism rates (Rudolf 2007). In such a scenario, cannibalism could make the invasion of the IG prey more difficult if the predator ( $P_A^*$ ) density increases faster than the resource density ( $R^*$ ), but this will depend on the specific relative parameter values. Numerical simulations showed that the resource will generally increase much faster than the predator population (Rudolf 2007).

The effect of enrichment (i.e., increasing  $K$ ) on the extinction of the IG prey can be derived by reversing the inequality in Eq. 6. The equilibrium conditions for  $R^*$  and  $P_A^*$  (see Appendix) indicate that, without cannibalism ( $\beta = 0$ ), enrichment of the system will lead to an increase in the predator,  $P_A^*$ , while  $R^*$  remains constant (see Appendix), thus ultimately leading to the extinction of the IG prey driven by the numerical increase in the

population of the IG predator (Fig. 3a). With cannibalism, however, both  $R^*$  and  $P_A^*$  increase with enrichment (Fig. 3b, c) and the explicit condition for extinction is

$$\theta\lambda(m + \mu_J) + \frac{r}{\alpha + \alpha'\lambda} [\theta\lambda\beta(1 - e_P) - h] - \mu_N < 0$$

with  $\theta = e_{RNA}/e_{RP}\alpha$  and  $\lambda = \mu_A/m$  (see Appendix). Thus, low cannibalism rates can still result in exclusion of the prey but this will occur at higher productivities (Fig. 3b). When the mortality due to cannibalism is larger than the intraguild predation [i.e.,  $\lambda\beta(1 - e_P) \geq h$ ], however, the prey cannot be excluded by the predator as long as the prey is at least as efficient in exploiting the resource as the predator (i.e.,  $\theta \geq 1$ ; Fig. 3c). Increasing the maturation rate,  $m$ , decreases the mortality due to cannibalism and thus requires a higher cannibalism rate to prevent the extinction of the IG prey. Similarly, increasing the IG predator efficiency in exploiting the resource also requires higher cannibalism rates to prevent prey extinction. Note that this is consistent with condition (4) given above. Furthermore, both results indicate that if the IG predator can be more efficient ( $e_{RP}\alpha > e_{RPA}$ ) it also can invade a system at a lower resource density than the IG prey, followed by the subsequent invasion of the prey into the two-species R–P system at higher productivity (Fig. 3c). The reason for this is that with cannibalism in the IG predator, the abundance of the resource increases with enrichment, while it remains constant when the predator is not cannibalistic (Rudolf 2007). This increase in the resource also increases the reproductive rate of the IG prey and eventually enables the IG prey to invade the R–N system depending on the specific conditions. Note that this condition also implies that as long as the predator is more efficient in exploiting the resource, the predator does not need to gain substantially from predation to coexist with the prey as required in non-cannibalistic models.

*Cannibalism in the IG prey*

The system with cannibalism in the prey and linear functional responses is

$$\frac{dR}{dt} = R \left[ r \left( 1 - \frac{R}{K} \right) - aN_A - a'N_J - \alpha P \right] \tag{7a}$$

$$\frac{dN_J}{dt} = N_A [e_{RNA}R + (e_N - 1)\beta N_J] - (h'P + m + \mu_J)N_J \tag{7b}$$

$$\frac{dN_A}{dt} = mN_J - N_A(\mu_A + hP) \tag{7c}$$

$$\frac{dP}{dt} = P(e_{RP}\alpha R + e_{NAP}hN_A + e_{NJP}h'N_J - \mu_P). \tag{7d}$$

An analysis similar to the previous scenario shows that the condition for the successful invasion of the predator into the  $C^*$ ,  $R^*$  system depends on the

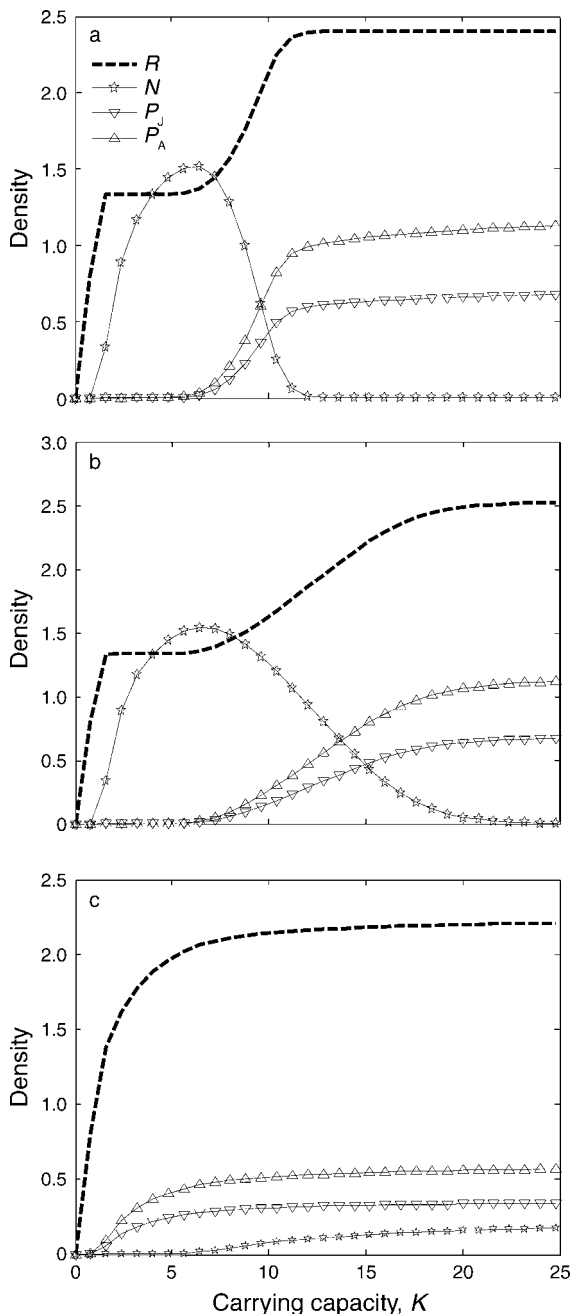


FIG. 3. Effect of enrichment and cannibalism on the coexistence (density) of the predator ( $P$ ), prey ( $N$ ), and resource ( $R$ ). In the first two scenarios, the prey is the superior competitor (a) without cannibalism ( $\beta = 0$ ), and (b) with low cannibalism ( $\beta = 0.015$ ) rates in the predator. In both cases, the predator drives the prey to extinction at higher resource productivity. (c) With large enough cannibalism rates ( $\beta = 0.5$ ), the predator can be superior in resource exploitation, invading at lower resource density than the prey, and does not drive the prey to extinction. Parameter values are:  $r = 0.4$ ,  $K = 2$ ,  $\alpha = 0.2$ ,  $e_{RP} = 0.2$ ,  $h = 0.05$ ,  $e_{NP} = 0.5$ ,  $e_P = 0.5$ ,  $m = 0.1$ ,  $\mu_N = \mu_{PA} = \mu_{PJ} = 0.06$ ; (a)  $e_{RN} = 0.225$ ,  $\beta = 0$ ,  $\alpha = \alpha' = 0.2$ ; (b)  $e_{RN} = 0.225$ ,  $\beta = 0.015$ ,  $\alpha = \alpha' = 0.2$ ; (c)  $e_{RN} = 0.2$ ,  $\beta = 0.5$ ,  $\alpha = 0.4$ ,  $\alpha' = 0.3$ . Parameters are defined in Table 1.

cannibalism rate in the prey. The invasion condition for the IG predator is  $e_{\text{RP}}\alpha R^* + (e_{\text{NAP}}h + e_{\text{NJP}}h'\lambda)N_A^* - \mu_P > 0$  (see Appendix). Increasing the cannibalism rate increases the resource density at equilibrium,  $R^*$  ( $dR^*/d\beta > 0$ ) but it decreases the IG prey density,  $N_A^*$  ( $dN_A^*/d\beta < 0$ ). Thus, the influence of cannibalism on the invasion condition of the IG predator depends on the net effect of the changes in the cannibalism rate on its reproductive output (see Appendix). If the total reproductive output of the IG predator depends mostly on the consumption of the resource ( $e_{\text{RP}}\alpha \gg e_{\text{NAP}}h + e_{\text{NJP}}h'\lambda$ ), cannibalism will facilitate the invasion of the predator. The reverse is true, however, if the reproductive output of the IG predator is largely dependent on the IG prey.

As in the previous case, cannibalism has no effect on the invasion condition of the cannibalistic species itself. The prey can invade the  $R^* - P^*$  system at equilibrium if  $me_{\text{RN}}a\mu_P/e_{\text{RP}}\alpha - (h'(1 - \mu_P/e_{\text{RP}}\alpha K)r/\alpha + m + \mu_J)(\mu_A + h(1 - \mu_P/e_{\text{RP}}\alpha K)r/\alpha) > 0$ . This shows that increasing the productivity of the resource makes invasion of the prey more difficult and there is always some level of  $r$  above which the prey will become extinct. Decreasing the vulnerability of either the adult or juvenile stage of the prey ( $h$  or  $h'$ ) will generally result in extinction of the prey at higher productivity levels and thus increase the region of coexistence of predator and prey.

#### TOP-DOWN CASCADES

The effect of changing the mortality and thus the abundance of the IG predator on the bottom resource was examined using extensive numerical simulations exploring a large parameter space. Results show that the effect of this top-down cascade depends on the specific scenario. If only the IG predator is cannibalistic, increasing the IG predator mortality will always have a negative effect on the resource abundance, even if the predator is more efficient in exploiting the resource than the prey. However, increasing the cannibalism rate reduces the rate at which the resource decreases, weakening the top-down cascade.

If the IG prey is cannibalistic, however, increasing the mortality of the predator does not necessarily lead to a decrease in resource density but can result in the opposite effect and increase the density, even though the prey has to be a superior exploiter of the resource in this scenario. The simulations show that depending on the specific parameter combinations, the resource increases with increasing IG predator mortality if the cannibalism rate is large enough relative to the other attack rates (Fig. 4). If the competitive ability of the IG predator is increased relative to the IG prey (i.e.,  $\alpha$  relative to  $a, a'$ ), lower cannibalism rates are required for this positive effect to occur. However, increasing the intraguild predation rate on either one or both IG prey stages ( $h, h'$ ) requires higher cannibalism rates for this positive effect to occur. Thus, if only one stage is invulnerable to predation, the positive effect is more

likely. In general, increasing the mortality of the IG predator is most likely to result in an increase in the bottom resource (R) if the cannibalism rate is large relative to the intraguild predation rate and if the IG predator is only a slightly inferior competitor. The reason for this positive effect is that cannibalism effectively introduces an additional trophic level into the system: the decrease in intraguild predation and thus mortality of the IG prey is compensated for by the increase in IG prey mortality due to cannibalism.

#### DISCUSSION

The models presented here show that introducing cannibalism, a common feature of natural food webs and IGP systems, can greatly alter the conditions for coexistence and the structure and dynamics of food webs expected from simpler models without cannibalism (Holt and Polis 1997). This suggests that including cannibalism, a common ecological interaction, into current food web models can overcome the discrepancy between theory and empirical data.

#### *Coexistence of IG predator and prey*

The results shown here indicate that cannibalism can greatly alter the conditions for coexistence of the IG predator and IG prey and the region of their coexistence across a productivity gradient. Current theory generally predicts that the predator has to be less efficient in exploiting the resource for both prey and predator to coexist (Holt and Polis 1997, Diehl and Feissel 2000, Mylius et al. 2001). Results presented here and in previous models (Mylius et al. 2001) show that adding solely a stage structure within either the predator or the prey did not alter these conditions. Several empirical studies, however, have shown that predators are often more efficient than their prey (Diehl 1995, Navarrete et al. 2000, Crumrine and Crowley 2003, Vance-Chalcraft et al. 2007). The model developed here predicts that predator-prey coexistence is possible under this scenario with a certain minimum degree of cannibalism in the predator. Since predators are often highly cannibalistic (Polis 1981, Polis et al. 1989), this could explain the observed higher efficiency in resource exploitation of the predator. Furthermore, the models show that cannibalism in the predator can also alter the effect of enrichment enabling the predator to persist at lower resource productivity than the IG prey and preventing the predator mediated extinction of the prey at high resource availability.

In general, the models predict that the effect of cannibalism on the region of coexistence of all three species largely depends on the trophic position where cannibalism occurs. Across systems, the likelihood of cannibalism in the IG prey vs. IG predator as cannibalism seems to be equally likely due to the high frequency at different trophic levels, although there could be some habitat-specific differences (Fox 1975). However, the positive effect of cannibalism in the

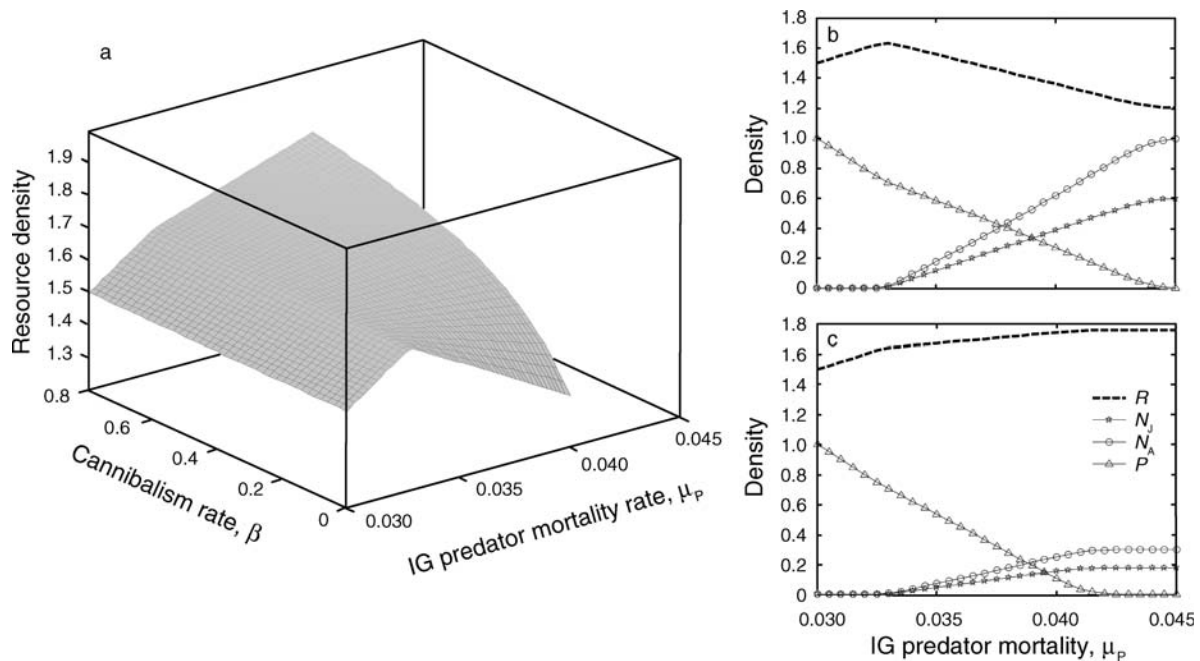


FIG. 4. Top-down effects of changes in the predator mortality ( $\mu_P$ ). (a) Effects of changes in the predator mortality on resource density ( $R$ ) depending on the cannibalism rates. Two examples of the corresponding changes in resource, prey, and predator density are shown (b) without cannibalism ( $\beta=0$ ) and (c) with cannibalism ( $\beta=0.5$ ). Parameter values are:  $r=0.4$ ,  $K=2$ ,  $a=a'=0.1$ ,  $h=0.01$ ,  $h'=0.05$ ,  $e_{RN}=0.8$ ,  $e_{RP}=0.2$ ,  $e_{NAP}=e_{NJP}=0.5$ ,  $e_N=0.5$ ,  $m=0.1$ ,  $\mu_P=0.04$ ,  $\mu_{NA}=\mu_{NJ}=0.06$ . Parameters are defined in Table 1.

predator on predator–prey coexistence regions is generally stronger than the negative effect of cannibalism in the prey on the coexistence region. This suggests that, even in systems where cannibalism occurs within both trophic levels, cannibalism is likely to increase the parameter space over which the three-species equilibrium persists, thus facilitating the coexistence of the predator and prey. Since cannibalism is a prominent feature of IGP systems (Polis et al. 1989, Woodward and Hildrew 2002), this could explain why IGP systems are stable and prevalent in natural communities (Polis et al. 1989, Arim and Marquet 2004). The precise predictions should be easily testable in future empirical studies.

#### *Top-down cascades in IGP systems*

Previous models generally suggested that the presence of the predator has a positive effect on the density of the shared resource. While some empirical studies seem to confirm this prediction, more studies show either no effect or a negative effect on the resource (reviewed in Diehl 1993, Rosenheim et al. 1993). The results presented here show that all three outcomes are possible, depending on the strength of cannibalism in the prey. This is consistent with previous unstructured models with density-dependent mortality (Polis et al. 1989) and supported by current empirical data. Contrary to what intuition might suggest, the direction of the resource's response (positive or negative) does not depend on the relative resource use efficiency of the predator and prey,

but rather on the strength of the cannibalism rate relative to the intraguild predation rate and on the trophic position at which cannibalism occurs. This prediction is supported by current empirical data. For example, in the 15 IGP systems reviewed by Diehl (1993), nine out of 12 systems that showed a negative relationship between resource density and presence of the predator included cannibalistic prey. Unfortunately, many of these studies were short-term experiments, yet long-term data are required to reliably test these predictions (Briggs and Borer 2005).

Cannibalism itself represents a specific form of omnivory (or IGP). It introduces a trophic structure within a species and increases the heterogeneity within the trophic levels and several parallels can be drawn to multi-species systems. In more diverse systems, the vertical and horizontal diversity across and within trophic levels strongly affects the direction and strength of trophic cascades (Leibold et al. 1997). Several empirical and theoretical studies have demonstrated that such trophic heterogeneity often weakens the direct and indirect interaction strength between species which in turn is likely to increase food webs stability and species persistence (Abrams 1993, Leibold et al. 1997, McCann and Hastings 1997, McCann et al. 1998, Finke and Denno 2004, Duffy et al. 2005). Interestingly, Persson (1999) pointed out in a recent review that much of the horizontal heterogeneity within natural food webs largely results from the size structure within popula-

tions. However, when and how the dynamics of systems with such size-structure heterogeneity differ from the dynamics of systems with heterogeneity due to species diversity is still poorly understood.

#### *Cannibalism vs. IGP*

In general, the models presented here suggest that the relative strength of cannibalism and intraguild predation largely determines the conditions for coexistence and the effect of enrichment. To date, few studies have quantified cannibalism rates, most likely because previous theory has not identified or emphasized the importance of cannibalism in shaping the dynamics of systems. The limited available data suggest that the relative strength of cannibalism and intraguild predation rate varies even across closely related species. For example in ladybird beetles, *Anolis* lizards, and plethodontid stream salamanders, some species show a higher attack rate for heterospecifics than conspecifics, while others show no difference, or a much higher attack rate for conspecifics (Gerber and Echternacht 2000, Yasuda et al. 2001, Burgio et al. 2005; V. Rudolf, *unpublished manuscript*). This variation could explain the different relationship between the predator, prey and resource abundances observed in the diverse IGP systems.

Although this study does not examine nonlinear functional responses in detail, most of the predicted general patterns are likely to hold true for a functional response with saturation. In previous studies, nonlinear functional responses did not alter the general coexistence predictions derived from linear functional responses (Holt and Polis 1997, Mylius et al. 2001, Revilla 2002). However, systems with nonlinear functional responses are more likely to result in bi-stability and alternative stable states (Holt and Polis 1997, Mylius et al. 2001, Revilla 2002). Future studies that examine the dynamics of IGP systems with cannibalism and different functional responses will provide important insight into the population dynamics of the species involved.

#### *Conclusions*

Surprisingly, although cannibalism is ubiquitous in natural food webs (Polis 1981, Woodward and Hildrew 2002), it still remains a highly understudied subject, especially considering its demonstrated importance for the dynamics and structure of communities and entire ecosystems (Persson et al. 2003). Recent empirical and theoretical studies have provided important insight into the effect of stage-structured interactions and cannibalism on community dynamics (Claessen et al. 2002, Hart 2002, Persson et al. 2003, Crumrine 2005, Rudolf 2006, 2007). However, these studies are few and are generally focused on cannibalism in the predator ignoring that cannibalism also commonly occurs at lower trophic levels, where species are subject to predation themselves. Thus, we still lack a basic understanding of the importance of cannibalism for community structure and dynamics, and there is a strong need for empirical

studies that focus on the effect of cannibalistic interactions at different trophic levels and its importance relative to interspecific predation.

#### ACKNOWLEDGMENTS

I thank H. M. Wilbur, J. Antonovics, M. A. McPeck, D. Roach, A. E. Dunham, and C. Bagdassarian for critical comments on earlier versions of the manuscript, S. Schreiber for mathematical advice, and J. A. Rosenheim for turning a lunch discussion into an organized Special Feature. This work was supported by the Ecology and Evolution Program of the University of Virginia.

#### LITERATURE CITED

- Abrams, P. A. 1993. Effect of increased productivity on the abundances of trophic levels. *American Naturalist* 141:351–371.
- Arim, M., and P. A. Marquet. 2004. Intraguild predation: a widespread interaction related to species biology. *Ecology Letters* 7:557–564.
- Briggs, C. J., and E. T. Borer. 2005. Why short-term experiments may not allow long-term predictions about intraguild predation. *Ecological Applications* 15:1111–1117.
- Burgio, G., F. Santi, and S. Miani. 2005. Intra-guild predation and cannibalism between *Harmonia axyridis* and *Adalia bipunctata* adults and larvae: laboratory experiments. *Bulletin of Insectology* 58:135–140.
- Claessen, D., A. M. De Roos, and L. Persson. 2004. Population dynamic theory of size-dependent cannibalism. *Proceedings of the Royal Society of London Series B* 271:333–340.
- Claessen, D., C. Van Oss, A. M. de Roos, and L. Persson. 2002. The impact of size-dependent predation on population dynamics and individual life history. *Ecology* 83:1660–1675.
- Crumrine, P. 2005. Size structure and substitutability in an odonate intraguild predation system. *Oecologia* 145:132–139.
- Crumrine, P. W., and P. H. Crowley. 2003. Partitioning components of risk reduction in a dragonfly–fish intraguild predation system. *Ecology* 84:1588–1597.
- Diehl, S. 1993. Relative consumer sizes and the strengths of direct and indirect interactions in omnivorous feeding relationships. *Oikos* 68:151–157.
- Diehl, S. 1995. Direct and indirect effects of omnivory in a littoral lake community. *Ecology* 76:1727–1740.
- Diehl, S. 2003. The evolution and maintenance of omnivory: dynamic constraints and the role of food quality. *Ecology* 84:2557–2567.
- Diehl, S., and M. Feissel. 2000. Effects of enrichment on three-level food chains with omnivory. *American Naturalist* 155:200–218.
- Diehl, S., and M. Feissel. 2001. Intraguild prey suffer from enrichment of their resources: A microcosm experiment with ciliates. *Ecology* 82:2977–2983.
- Duffy, J. E., J. P. Richardson, and K. E. France. 2005. Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. *Ecology Letters* 8:301–309.
- Fagan, W. F. 1997. Omnivory as a stabilizing feature of natural communities. *American Naturalist* 150:554–567.
- Finke, D. L., and R. F. Denno. 2004. Predator diversity dampens trophic cascades. *Nature* 429:407.
- Fox, L. R. 1975. Cannibalism in natural populations. *Annual Review of Ecology and Systematics* 6:87–106.
- Gerber, G. P., and A. C. Echternacht. 2000. Evidence for asymmetrical intraguild predation between native and introduced *Anolis* lizards. *Oecologia* 124:599.
- Hart, D. R. 2002. Intraguild predation, invertebrate predators, and trophic cascades in lake food webs. *Journal of Theoretical Biology* 218:111–128.
- Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. *American Naturalist* 149:745–764.

- Holyoak, M., and S. Sachdev. 1998. Omnivory and the stability of simple food webs. *Oecologia* 117:413–419.
- Leibold, M. A., J. M. Chase, J. B. Shurin, and A. L. Downing. 1997. Species turnover and the regulation of trophic structure. *Annual Review of Ecology and Systematics* 28: 467–494.
- McCann, K., and A. Hastings. 1997. Re-evaluating the omnivory-stability relationship in food webs. *Proceedings of the Royal Society of London Series B* 264:1249–1254.
- McCann, K., A. Hastings, and G. R. Huxel. 1998. Weak trophic interactions and the balance of nature. *Nature* 395: 794–798.
- Morin, P. 1999. Productivity, intraguild predation, and population dynamics in experimental food webs. *Ecology* 80:752.
- Mylius, S. D., K. Klumpers, A. M. de Roos, and L. Persson. 2001. Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *American Naturalist* 158:259–276.
- Navarrete, S. A., B. A. Menge, and B. A. Daley. 2000. Species interactions in intertidal food webs: Prey or predation regulation of intermediate predators? *Ecology* 81:2264–2277.
- Persson, L. 1999. Trophic cascades: abiding heterogeneity and the trophic level concept at the end of the road. *Oikos* 85: 385–397.
- Persson, L., P. Bystrom, and E. Wahlstrom. 2000. Cannibalism and competition in Eurasian perch: population dynamics of an ontogenetic omnivore. *Ecology* 81:1058–1071.
- Persson, L., A. M. De Roos, D. Claessen, P. Bystrom, J. Lovgren, S. Sjogren, R. Svanback, E. Wahlstrom, and E. Westman. 2003. Gigantic cannibals driving a whole-lake trophic cascade. *Proceedings of the National Academy of Sciences (USA)* 100:4035–4039.
- Pimm, S. L., and J. H. Lawton. 1978. On feeding on more than one trophic level. *Nature* 275:542.
- Polis, G. A. 1981. The evolution and dynamics of intraspecific predation. *Annual Review of Ecology and Systematics* 12: 225–251.
- Polis, G. A. 1984. Age structure component of niche width and intraspecific resource partitioning: Can age groups function as ecological species? *American Naturalist* 123:541–564.
- Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: Potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20:297–330.
- Revilla, T. 2002. Effects of intraguild predation on resource competition. *Journal of Theoretical Biology* 214:49–62.
- Rosenheim, J. A., L. R. Wilhoit, and C. A. Armer. 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia* 96:439–449.
- Rudolf, V. H. W. 2006. The influence of size-specific indirect interactions in predator–prey systems. *Ecology* 87:362–371.
- Rudolf, V. H. W. 2007. Consequences of stage-structured predators: cannibalism, behavioral effects, and trophic cascades. *Ecology* 88:2991–3003.
- Sih, A. 1981. Stability, prey density and age/dependent interference in an aquatic insect predator, *Notonecta hoffmanni*. *Journal of Animal Ecology* 50:625–636.
- Tanabe, K., and T. Namba. 2005. Omnivory creates chaos in simple food web models. *Ecology* 86:4311–4314.
- Vance-Chalcraft, H. D., J. A. Rosenheim, J. R. Vonesh, C. W. Osenberg, and A. Sih. 2007. The influence of intraguild predation on prey suppression and prey release: a meta-analysis. *Ecology* 88:2689–2696.
- Woodward, G., and A. G. Hildrew. 2002. Body-size determinants of niche overlap and intraguild predation within a complex food web. *Journal of Animal Ecology* 71:1063–1074.
- Yasuda, H., T. Kikuchi, P. Kindlmann, and S. Sato. 2001. Relationships between attack and escape rates, cannibalism, and intraguild predation in larvae of two predatory ladybirds. *Journal of Insect Behavior* 14:373.

#### APPENDIX

Analytical derivations of the effects of cannibalism and enrichment on the invasion conditions of the predator and prey (*Ecological Archives* E088-165-A1).