ALTERNATIVE PREY AND THE DYNAMICS OF INTRAGUILD PREDATION: THEORETICAL PERSPECTIVES

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Abstract. A rich body of theoretical literature now exists focused on the three-species module of intraguild predation (IGP), in which a top predator both attacks and competes with an intermediate predator. Simple models of intraguild predation are often unstable, either because one consumer is excluded, or because sustained oscillations emerge from long feedback loops. Yet, many natural IGP systems robustly persist. Standard models of intraguild predation simplify natural systems in crucial ways that could influence persistence; in particular, many empirical IGP systems are embedded in communities with alternative prey species. We briefly review the key conclusions of standard three-species IGP theory, and then present results of theoretical explorations of how alternative prey can influence the persistence and stability of a focal intraguild predation interaction.

Key words: alternative prey; asymmetry; community modules; intraguild predation.

INTRODUCTION

A tension exists in ecology between the desire to craft simple theories, and the recognition that nature is complex in many ways not captured in our models. This is particularly the case in community ecology. Communities contain thousands of species, interacting in a myriad of complicated ways. One approach that has proven fruitful is to focus on small sets of species strongly interacting in defined configurations: community modules (Holt 1997) such as food chains, apparent competition, and intraguild predation. Sometimes these simplifications lead to insights robustly relevant to much more complex systems. But in others, the simplifications turn out to be oversimplifications. For example, predictions about the pattern of abundance along productivity gradients as a function of trophic level, derived from linear food chain models (e.g., Oksanen et al. 1981), break down with multiple species at each level (Abrams 1993). Insights gleaned from simple theories need to be tested against a wide range of alternative model formulations, to distinguish general insights from those only narrowly applicable to particular systems.

Consider intraguild predation, defined as predator–prey interactions among consumers potentially competing for limiting resources. There is a rich and growing literature highlighting the importance of intraguild predation in natural communities (this Special Feature). The simplest model of intraguild predation involves

three species: a top predator (IG predator), an intermediate consumer (IG prey), and a shared resource. Holt and Polis (1997) explored several simple models for this three-way interaction, which for convenience we dub "basic intraguild predation" (Fig. 1A). This study sparked considerable attention (e.g., >160 citations as of January 2007) and empirical tests (e.g., Borer et al. 2003). Some empirical studies confirm predictions of simple theory, but others do not. One reason may be that in empirical systems, there are often more species involved in intraguild predation than just the three of the basic module (e.g., Rosenheim and Wilhoit 1993), potentially explaining why simple theories fail (Briggs and Borer 2005). Indeed, food web descriptions (e.g., Woodward et al. 2005) usually reveal that triads of species potentially engaged in IGP are also interacting with multiple resource and predator species. Here, we explore how conclusions from simple models of basic intraguild predation are affected when the simple three-species IGP module is embedded in richer communities. After sketching the key conclusions of Holt and Polis (1997), we add alternative resources in several model formulations and explore how the Holt-Polis conclusions are altered. We refer to this expanded module as "partial IGP" (Fig. 1C), as there is only partial overlap between predators in shared resources. We consider elsewhere (G. R. Huxel and R. D. Holt, *unpublished manuscript*) the effect of increasing the diversity of IG prey and IG predator species (Fig. 1B). Our purpose here is to make conceptual points about multispecies IGP, not to focus explicitly on comparisons of theory with empirical systems. Moreover, we do not fully explore the behavior of the models we discuss, but use a few salient results to illustrate general conceptual messages.

Intraguild predation modules

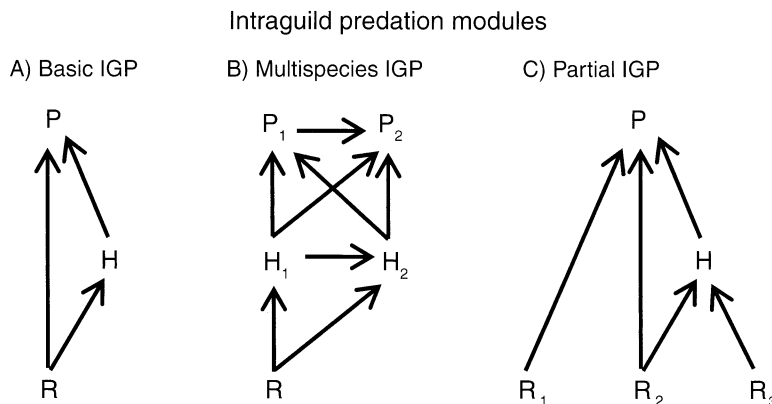A) Basic IGP   B) Multispecies IGP   C) Partial IGP

FIG. 1. Community modules with intraguild predation (IGP): (A) basic intraguild predation; (B) multispecies intraguild predation; (C) partial intraguild predation. The arrows go from prey to predator. R denotes a resource population, H an intermediate consumer (which could be a herbivore in some cases), and P a top predator. The numerical subscripts denote species at the same trophic level.

Key predictions of simple models

The results of Holt and Polis (1997) provide yardsticks for gauging the impact of alternative resources. Their first generalized resource–consumer model led to several qualitative predictions: (1) a necessary condition for robust coexistence in IGP (so each species increases when rare) is that the IG prey should be superior in competition, as assessed by the R^* rule; (2) for coexistence, the top species (the IG predator) should gain significant fitness benefits from consumption of the IG prey; (3) the IG predator indirectly increases the equilibrial abundance of the shared resource (a trophic cascade). Their second model was a Lotka-Volterra model in which the resource had logistic growth, and the two consumers had linear functional and numerical responses. This more detailed model predicted that (4) along gradients of increasing productivity, dominance should shift from IG prey to IG predator, with coexistence at intermediate levels; (5) alternative stable states occur; (6) mutual invasibility may not ensure long-term persistence due to unstable dynamics, pushing populations to low densities. This instability emerges from a long feedback loop linking the resource, IG prey, and IG predator (Tanabe and Namba 2005).

IGP with alternative prey

A general "additive" model of intraguild predation with alternative resources is as follows (resource equations are not needed for the points made below):

$$\frac{dP}{dt} = P\{f_P(R,R_P) + g_P[\alpha(P,N,R)N]\} \quad \text{(IG predator)}$$

$$\frac{dN}{dt} = N[f_N(R,R_N) - \alpha(P,N,R)P] \quad \text{(IG prey).} \quad (1)$$

The f terms describe the growth of each consumer on the shared (at density R) and exclusive (at densities R_N, R_P) resources; α is the death rate of the IG prey due to each

IG predator; and g_P is additional growth the IG predator enjoys from this consumption. We assume that each species' growth rate increases with the abundance of its resources. For the system in Eq. 1 to have an equilibrium with coexistence, the IG predator must have a negative growth rate on all resources other than the IG prey, and the IG prey needs a positive growth rate on its own resources offsetting mortality inflicted by the IG predator. If the shared resource is the *only* resource in the system, then Holt and Polis (1997) argue this implies that the IG prey is superior in exploitative competition for this resource, by the usual R^* criterion (Tilman 1977).

Adding alternative resources for the IG predator strengthens this expectation. If the IG predator is superior in competing for the shared resource, its R^* (for that resource) will be lower than that of the IG prey; alternative prey at equilibrium indirectly push the shared resource below this R^* (Holt 1977). If the IG prey is an inferior competitor without the alternative prey for the IG predator, it will continue to be an inferior competitor with such prey. Hence, for coexistence the IG prey must still be superior at competing for the shared resource. However, to persist, the IG predator need not benefit at all from its attacks on the IG prey, given sufficient, high-quality, exclusive resources. When the IG prey has exclusive resources, its persistence in turn does not depend on being superior at all in competing for the shared resource. To illustrate this point, we return to the Lotka-Volterra IGP model in Holt and Polis (1997; notational differences), with equations for exclusive resources:

Shared resource:

$$\frac{dn_1}{dt} = (b_1 - a_{11}n_1 - a_{12}n_2 - a_{13}n_3)n_1$$

IG prey:

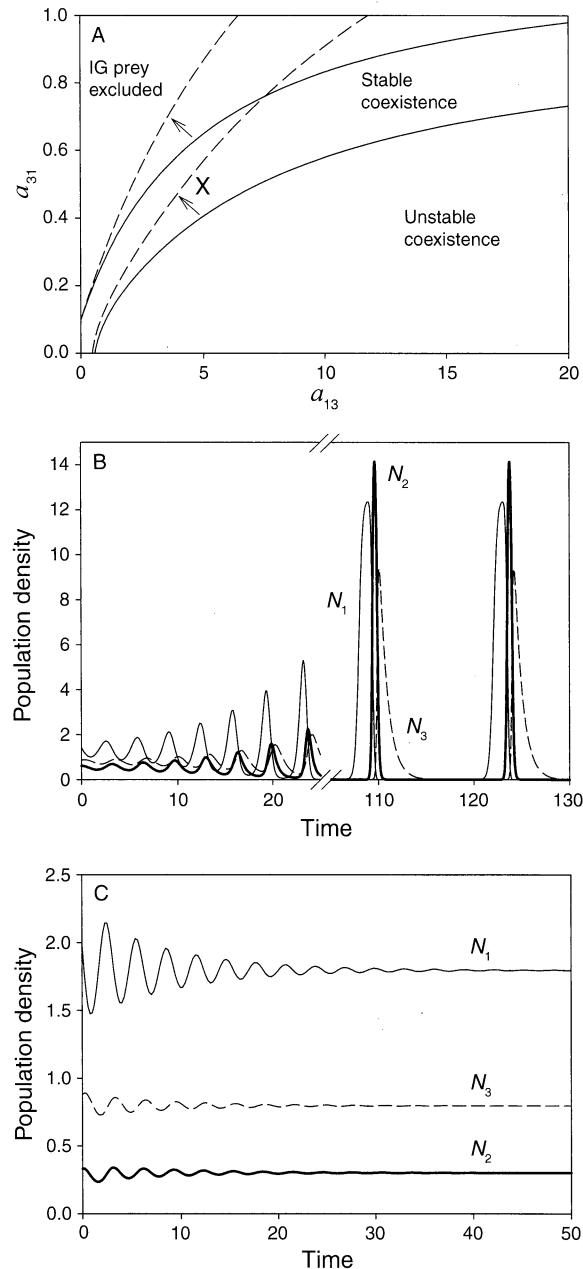$$\frac{dn_2}{dt} = (-b_2 + a_{21}n_1 - a_{23}n_3 + a_{24}n_4)n_2$$

FIG. 2. Effect of alternative prey via changes in IG prey death rate: a_{13} is the attack rate of the IG predator on the resource; a_{31} is the increase in IG predator birth rate due to resource consumption. (A) Solid lines delineate regions of exclusion, stable, and unstable coexistence, with $b_2 = 1$, $b_1 = 5$, $b_3 = 1.2$, $a_{11} = 0.4$, and $a_{12} = a_{21} = a_{23} = a_{32} = 1$. Dashed lines show the shift in these regions when IG prey death rate is reduced to $b_2 = 0.5$. Figs. 2–4 and those in the Appendices were generated using standard invasibility and numerical Routh-Hurwitz analyses. (B and C) Population dynamics for $a_{13} = 5$, $a_{31} = 0.5$ (X in panel A); with (B) $b_2 = 0.5$ or (C) $b_2 = 1.0$. Parameters are b_i, intrinsic rates of growth or decline; a_{ii}, the strength of density dependence in resource i; and N_i, the density of the appropriate trophic level. Solid lines in panel (A) match Tanabe and Namba (2005).

IG predator:

$$\frac{dn_3}{dt} = (-b_3 + a_{31}n_1 + a_{32}n_2 + a_{35}n_5)n_3$$

Exclusive resource for IG prey:

$$\frac{dn_4}{dt} = (b_4 - a_{42}n_2 - a_{44}n_4)n_4$$

Exclusive resource for IG predator:

$$\frac{dn_5}{dt} = (b_5 - a_{53}n_3 - a_{55}n_5)n_5. \tag{2}$$

Here, the b_i are intrinsic rates of growth or decline; a_{ii} is the strength of density dependence in resource i; and a_{ij} measures the per capita effect of species j on species i.

Before presenting some results for the model in Eq. 2, it is worth remarking that alternative resources need not require additional dynamical equations. For instance, a consumer might utilize a low-quality resource whose standing crop is rapidly renewed. If consumption has a negligible effect upon resource abundance, there is no exploitative competition for that resource. In this case, the effect of the alternative resource is via an increase in the consumer's intrinsic growth rate (e.g., its death rate might be reduced). Such shifts in density-independent growth rates can have important dynamical consequences. Fig. 2 shows an example. An alternative resource that reduces the death rate of the IG prey helps it to tolerate a broader range of attack rates from the IG predator. In this example, the zone of parameter space leading to unstable dynamics also expands (see Fig. 2B, C). Thus, adding an alternative prey species to intraguild predation can permit coexistence, but it can also be destabilizing.

Briggs and Borer (2005) suggest the impact of alternative prey can be mimicked by adding a subsidy term (comparable to immigration) to the IG predator and IG prey equations. Such subsidies for the IG predator alone make coexistence more difficult; subsidies for the IG prey, by contrast, prevent its extinction in the face of intraguild predation. Because subsidies add an additional component of direct density dependence, given that coexistence occurs it is likely to be stabilized by substantial subsidies, rather than show cycles or chaos. By contrast, alternative prey that boost density-independent growth can be destabilizing (Fig. 2B) and may not suffice to prevent extinction (Fig. 2A).

More generally, one might expect the abundance of alternative resources that are exclusively available to a consumer to respond dynamically to consumption (as in Eq. 2). Because there are now additional species with their own dynamics, there are new issues that need to be sorted through regarding species coexistence, and additional feedback loops that can influence stability. We will assume that the alternative prey can persist; this leaves open the issue of how alternative prey influence the persistence of the shared prey, as well as the coexistence of the IG predator and IG prey. If

alternative prey indirectly drive extinct the shared prey, the basic intraguild predation module disappears. Adding new resource species (not competing with previous resources) in effect increases productivity. So as not to confound changes in productivity with changes in species richness, we assume that the total resource carrying capacity is fixed and examine how the partitioning of this resource base between shared and exclusive resources influences coexistence and stability. There are several distinct ways one could partition the resource base. In the examples shown, we assume all resources have the same intrinsic growth rate and so differ in carrying capacity due to differences in direct density dependence (the a_{ii} parameters). The dimensionality of the model precludes a full formal analysis, so we present illustrative cases.

Assume the IG prey alone has exclusive resources. Fig. 3 depicts how coexistence depends on the IG prey's attack rate and the fraction of exclusive resources, for two different productivity levels. In this example, without an exclusive resource for the IG prey there is no coexistence. The IG prey is vulnerable to exclusion if its attack rate on the resources is low, and it has relatively little exclusive resource. The IG predator may in turn be excluded if the IG prey has an exclusive resource, and the IG prey has a high attack rate, particularly at low productivity (Fig. 3B). As makes intuitive sense, providing alternative resources for the IG prey can facilitate coexistence (as suggested in the discussion of Holt and Polis 1997). Increasing the amount of exclusive resource available to the IG prey reduces the attack rate on the shared resource required for it to persist. Thus, the conclusion of Holt and Polis (1997) for the basic IGP module that the IG prey should be superior at competition for the shared resource clearly fails if the IG prey has exclusive resources (Fig. 1C; see also Briggs and Borer 2005). Coexistence occurs for intermediate ranges of attack rates for the IG prey, when it has substantial exclusive resources; in the specific example shown, such resources are required for coexistence. The reason for coexistence only at intermediate attack rates by the IG prey is that when the shared resource is scarce, the IG predator only persists if the IG prey is sufficiently abundant, which in turn requires the IG prey have sufficient attack rates on its own prey. But high attack rates by the IG prey permit its over-exploitation of its resources, depressing its own abundance, thus making the environment resource poor for the IG predator. An increase in productivity shifts the system so as to favor the IG predator (Fig. 3B has lower total resource, K, than does Fig. 3A). The general conclusion of Holt and Polis (1997) that increased productivity tilts a system toward dominance by the IG predator still holds, at least in this example (see Appendix B).

With alternative resources for the IG prey, it becomes more difficult for the shared resource to persist because of apparent competition, and there can be emergent
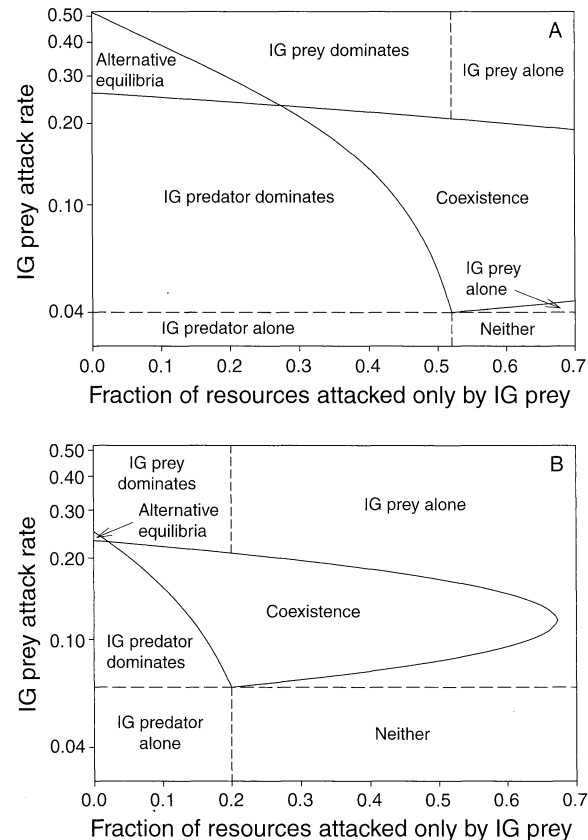

Fig. 3. Regions of coexistence, exclusion, and alternative equilibria when the IG prey has an exclusive resource, as a function of its attack rates. Summed carrying capacity of both resources is fixed at K; the two resources are identical except for their carrying capacities (adjusted using the a_{ii}). The exclusive resource's fraction of total carrying capacity is the abscissa. The ordinate is attack rate of the IG prey ($a_{12} = a_{42}$); $b_1 = 5$, $b_2 = 1$, $b_3 = 1.2$, $a_{13} = 0.5$, $a_{31} = 0.1$, $a_{23} = 1$, and $a_{32} = 0.05$. (Densities are scaled so that $a_{12} = a_{21} = a_{24}$). If the IG predator dominates, the IG prey persists when alone; the label "alone" implies the other species cannot persist on the resources. (A) $K = 25$; (B) $K = 15$.

impacts upon dynamical behavior. Fig. 4A shows one example of how system behavior depends on the partitioning of resources between those shared and those exclusive to the IG prey. Without exclusive resources, coexistence requires the IG predator not have too high an attack rate on the shared resource. If this attack rate is lower, the system can exhibit strongly unstable dynamics (which in practice will lead to extinction). The presence of a modest amount of alternative resources for the IG prey makes it more difficult for it to be excluded by the IG predator, and so facilitates coexistence. But alternative resources can also destabilize otherwise stable systems; indeed, a substantial swath of parameter space exhibits such instability. With sufficient alternative resources, the shared resource is excluded: such exclusion is more likely when the IG predator has high attack rates on the shared resource. In
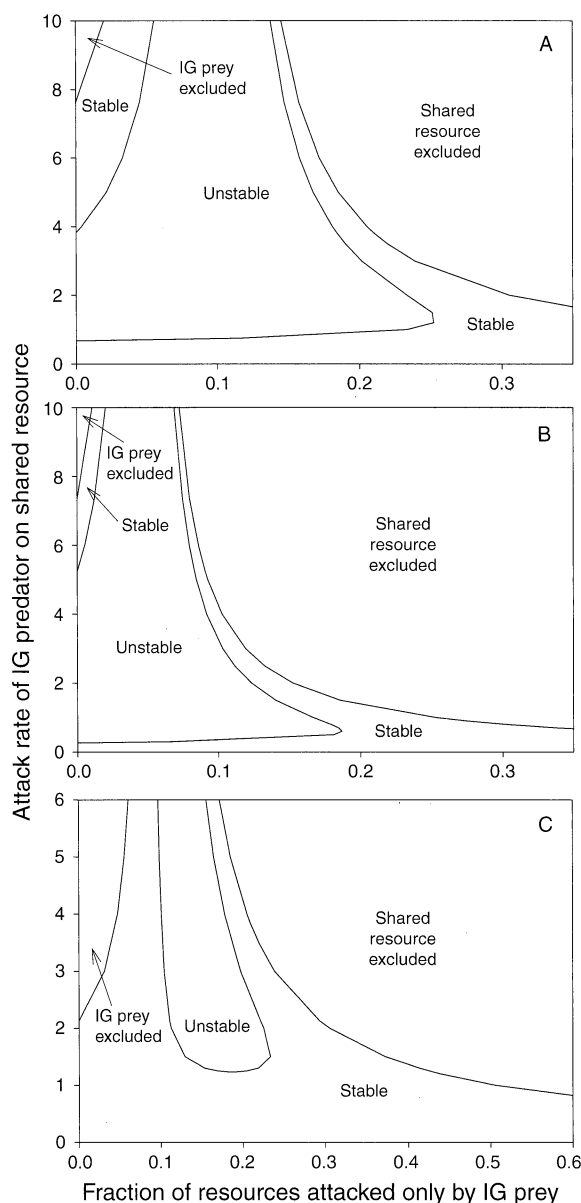
FIG. 4. Regions of coexistence, stability, and exclusion when the IG prey has an alternative resource, as a function of IG predator attack rates. Total K of the two resources is fixed, as in Fig. 3. Parameters are $b_1 = 5$, $b_2 = 1$, $b_3 = 1.2$, $a_{21} = a_{24} = a_{12} = a_{42} = 1$, and $a_{23} = a_{32} = 1$. We let $a_{31} = c_3 a_{13}$, and set $c_3 = 0.1$ in panels A and B. (A) $K = 12.5$ with all resources shared; the system and parameters match Fig. 1 (solid lines); (B) $K = 25$; (C) $K = 12.5$ and $c_3 = 0.2$.

this region of parameter space, intraguild predation has collapsed, not because the IG predator and IG prey cannot coexist, but because an alternative resource sustains them jointly at sufficient abundance to squeeze the shared resource out of the system. Fig. 4B is similar, but at a higher productivity. Increased productivity shifts the parameter domain leading to instability, and makes it more likely the shared resource will be excluded

by apparent competition. In the example of Fig. 4A, B, the IG predator gains only a moderate fitness benefit from consuming the resource. By comparison, in Fig. 4C, the IG predator enjoys a greater fitness benefit from consuming the resource. This makes exclusion of the IG prey more likely and somewhat reduces the instability domain. Thus the impact of alternative prey on stability depends upon the reciprocity of the interaction between IG predator and IG prey.

Some other scenarios are shown in the electronic appendices. Fig. A1 (in Appendix A) shows a slice through parameter space, where what varies is the IG prey's attack rate upon both resources. Again, alternative resources alter conditions for coexistence and stability. The shared resource can be eliminated if the alternative resource is common and the IG prey has a high attack rate. In this example, unlike those above, the alternative resource tends to stabilize dynamics. Fig. A2 (in Appendix A) turns the tables by allowing the IG predator to have exclusive resources. Not surprisingly, this makes it easier for the IG prey to be excluded. In this example an alternative resource for the IG predator reduces the lower bound of the coexistence bandwidth characterizing coexistence (as it is less likely that the IG predator itself will be excluded when it cannot utilize basal resources). Finally, Fig. A3 (in Appendix A) shows what can happen when both the IG predator and IG prey have exclusive resources. With only the shared resource, there is a modest range of IG prey attack rates that permit coexistence, often with unstable dynamics. With more exclusive resources, there is a much broader range of IG prey attack rates that leads to coexistence. But over much of the range of parameter space, the shared resource is excluded.

Nonlinear IGP modules

An important question regarding community modules is whether results are consistent across models differing in functional form, and in particular whether linear and nonlinear models give qualitatively similar results. A well-known limitation of Lotka-Volterra models is the assumption of linear functional responses. Introducing saturating responses into community models can weaken interactions and also leads to positive density dependence; this can induce instability, which in turn can allow either extinction due to excursions to low densities, or nonequilibrial competitive coexistence. Space constraints preclude a full treatment of nonlinear models, so here we simply mention a few illustrative, interesting effects emerging in nonlinear modules of IGP (for more details, see G. R. Huxel and R. D. Holt, *unpublished manuscript*).

Early studies of omnivory (including IGP; Pimm and Lawton 1978) using Lotka-Volterra models suggested that omnivory was generically destabilizing, but McCann and Hastings (1997) used nonlinear models to show that weak to moderate omnivory could stabilize otherwise unstable predator-prey interactions. Using the

same basic model structure as did they (see also McCann et al. 1998), we examined how conclusions from the above Lotka-Volterra IGP models changed given alternative prey and nonlinear (type II) functional responses. Three scenarios were investigated: (1) an alternative prey for the IG predator (a parameter ω_{42} measures the predator preference for alternative prey); (2) an alternative prey for the IG prey, with ω_{32} as a measure of preference by the IG prey; (3) both feeding on the alternative prey (the preference measures then describe niche partitioning between the IG predator and IG prey). The details are described in Appendix C, which also contains illustrative figures.

With an alternative prey for the IG predator, we chose parameters such that the system exhibits chaotic dynamics when ω_{42} is zero. Increasing ω_{42} leads to period doubling reversal, until a limit cycle develops. The IG prey becomes extinct at intermediate values for ω_{42}; the IG predator then exhibits a stable equilibrium (Appendix C: Fig. C1) and increases with ω_{42}. Eventually, the IG prey again coexists with the IG predator. Extinction of the IG prey at intermediate values of ω_{42} in part reflects reduced resource availability due to exploitative competition with the IG predator, and in part increased density of the IG predator due to the alternative prey. Thus a strong indirect apparent competition effect via alternative prey on the IG prey occurs and influences dynamics. (In this example, the basal and alternative resources both exhibit near-equilibrial dynamics due to the moderate interaction strengths of the omnivorous links.)

When only the IG prey consumes the alternative prey, both IG prey and IG predator exhibit shifting periodic dynamics including chaos as ω_{32} increases (Appendix C: Fig. C2), with increasing maxima and decreasing minima. Increasing ω_{32} (increasing preference for the alternative prey by the IG prey) in effect increases niche differentiation between the two consumers. The system is chaotic for intermediate values of ω_{32}, corresponding to a strong link between the IG prey and the basal resource. At higher values, the link between the IG prey and the basal species becomes weak and tends to act as a stabilizing factor, so the system moves into lower period oscillations. When both the IG prey and IG predator prey upon the alternative prey and ω_{42} is changed, the resulting dynamics resemble those seen when only the IG predator consumes the alternative prey (Appendix C: Fig. C3). The system is somewhat more stable than in the first scenario because of the stabilizing effect of the weak link between the IG prey and the alternative prey. The dynamics stabilize through period double reversals; however, the IG prey becomes extinct when the IG predator sufficiently increases its consumption of the alternative prey. The mechanisms that drive the IG prey extinct are the same as those for scenario 1. After extinction of the IG prey, the IG predator exhibits stable equilibria. Thus coexistence can depend on the existence of weak links between the IG predator and either the IG

prey (when ω_{42} is large) or the alternative prey (when ω_{42} is small). Increasing ω_{42} makes it less likely that one of the conditions for coexistence in the Holt and Polis (1997) model holds, namely that the IG predator gains significant fitness benefits directly from the IG prey. Instead, the interaction between the IG predator and the IG prey largely reflects apparent competition between the IG prey and the alternative prey species. In simulations with ω_{32} as the variable parameter, the system behavior resembles that of the second scenario (Appendix C: Fig. C4). The effect of the added link between the IG prey and the alternative prey here does not stabilize the dynamics, indeed the added link somewhat destabilizes the system (in that less of the parameter space exhibits low period oscillations). Nonetheless, coexistence is maintained across the entire range of ω_{32} values and so is not dependent upon the maintenance of weak links between the IG prey and the two basal species.

Conclusions and Future Directions

One of the virtues of simple models, such as those considered in Holt and Polis (1997), is that they provide a base of departure for gauging the influence of complicating and realistic features in ecological systems. Here we have used several models to point out how alternative prey can alter the predictions arising from models of simple IGP. It is useful to quickly summarize the main results we have presented, both in the main text and the Appendices. If the IG prey has exclusive resources, there is no reason in general to expect it to be superior in competing for the shared resource (see also Briggs and Borer 2005); however, if the IG prey is substantially inferior its persistence will require that it obtain a substantial part of its diet from alternative, non-shared resources (see Fig. 3). If the IG predator in turn has exclusive resources, the system can persist even if the IG predator receives little direct benefit from consuming the IG prey. Along productivity gradients, there is often still a shift in dominance from the IG prey to the IG predator (Appendix B). Alternative prey make it possible for the shared prey species to be excluded, in which case the formal conditions for IGP no longer hold. With both linear and nonlinear models, there are a variety of impacts upon stability. Increasing system complexity of the system by adding alternative prey increases the range of indirect effects in the community. Feedbacks on community dynamics due to apparent competition, omnivory, and niche differentiation all potentially play increasingly significant roles in more complex modules. Moreover, the addition of weak interactions can stabilize the systems, whereas adding relatively strong interactions tends to be destabilizing in terms of both population fluctuations and coexistence (McCann et al. 1998). In both linear Lotka-Volterra and nonlinear models of IGP, with and without alternative prey, given cycles or chaotic dynamics, densities often reach very low values where demographic stochasticity

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would likely nudge species toward local extinctions. For persistence, one then needs either to invoke factors not built into the above models (e.g., behavioral plasticity; see Heithaus 2001, Kimbrell et al., *in press*) or to embed local interactions into a metacommunity context where persistence arises from a balance between regional extinctions and colonizations. We suggest that an important direction for future work, in general, is to embed analyses of community modules into richer webs of interacting species, interacting across heterogeneous and patchy landscapes.

Note added in proof

Several authors have recently independently incorporated alternative prey into intraguild predation and reached conclusions complementing and paralleling our own (see Daugherty et al. 2007, Namba et al., *in press*).

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APPENDIX A

Supplementary examples of how alternative resources influence stability and coexistence in intraguild predation (*Ecological Archives* E088-166-A1).

APPENDIX B

Intraguild predation along productivity gradients (*Ecological Archives* E088-166-A2).

APPENDIX C

Effect of nonlinear (saturating) functional responses upon IGP dynamics (*Ecological Archives* E088-166-A3).