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WHY SHORT-TERM EXPERIMENTS MAY NOT ALLOW LONG-TERM PREDICTIONS ABOUT INTRAGUILD PREDATION

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Abstract. Equilibrium models are increasingly employed in applied ecology, but often because of experimental logistics, only short-term laboratory experiments are performed. Here, we use simple models to examine the management relevance of this disconnection between theory and experiments in communities with intraguild predation (IGP). Equilibrium theory shows that IGP can promote coexistence of competitors on a shared resource. However, adding the intraguild predator can result in higher resource densities than in a system with the intraguild prey alone with its resource. This has important management implications when the shared resource is a pest species whose population is controlled by natural enemies. Our models demonstrate why short-term experiments and studies ignoring alternate resources may bear no relationship to a system at equilibrium. Short-term experiments quantifying only attack rates can predict a broad range of outcomes. By ignoring conversion efficiency, consumer longevity, and immigration, short-term studies may, for example, cause erroneous decisions about the introduction of natural enemies in biological control. Thus, attack rates, conversion efficiencies, and immigration rates must all be quantified for a thorough, long-term understanding of IGP in field systems.

Key words: *biological control; closed system; conversion efficiency; equilibrium theory; immigration; invasive species.*

INTRODUCTION

Applied ecology has increasingly used mechanistic models of population dynamics to guide management decisions. This trend has led to many advances in both management and theory. A great strength of this approach is that models can provide long-term management predictions. Unfortunately, however, multigeneration experiments are often difficult to carry out, and long-term dynamic predictions are commonly extrapolated from short-term experiments (Brown et al. 2001, Hastings 2004). Here, we use simple models to demonstrate the management pitfalls of this disconnection between equilibrium theory and short-term experiments using a case study of intraguild predation. The theoretical implications of IGP are relevant to several interrelated issues currently facing community ecologists: invasive species, agricultural pests, commercially harvested natural resources, and biological control (e.g., Rosenheim 2001, MacNeil et al. 2003). Although the current paper is relevant to all communities with IGP, we focus here on biological control communities

because, more than any other area of ecology, the dynamic outcome of IGP on the basal resource, the pest, is of particular concern.

Intraguild predation (IGP), a form of omnivory, is a trophic interaction in which a species can prey on both its guild member and the resource it shares with that guild member (Polis et al. 1989). A recently published equilibrium model of IGP by Holt and Polis (1997) has spurred an explosion of empirical studies examining this phenomenon in a multitude of ecological communities. IGP theory predicts that if the intraguild prey (IG prey) is more effective than the intraguild predator (IG predator) at exploiting the basal resource then, at equilibrium, (a) all three species may coexist, but (b) the presence of the IG predator will cause a higher equilibrium density of the resource than that in a system with only the IG prey and the resource. For coexistence, the IG predator must realize fitness benefits from attacking the IG prey. These theoretical predictions are for systems at equilibrium in which the long-term densities of all three species result from the IGP interaction itself.

IGP is common among natural enemies of many agricultural pests, and depending on its importance in these communities, theory predicts that IGP between

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natural enemies of the pest may reduce the effectiveness of biological control (Rosenheim et al. 1995). This observation has led to an increasing awareness and quantification of the effects of IGP in biological control communities (Rosenheim et al. 1995, Rosenheim 1998, Brodeur and Rosenheim 2000, vanRijn et al. 2002). While empirical quantification is clearly an important step toward a predictive understanding of systems with IGP, a review of this literature suggests that there is a disconnection between the equilibrium predictions of IGP theory and the empirical examinations of the role of IGP in real communities. Although this disconnection between theory and empirical studies of IGP has been discussed previously (Brodeur and Rosenheim 2000, Venzon et al. 2001), here we explore the dynamic implications of two elements of this disconnection.

In particular, we use theory to examine the disconnection between closed-system, equilibrium IGP theory and empirical investigations. First, we briefly review a subset of empirical studies examining IGP and find that the majority of these studies are very short in duration relative to the generation times of the species under examination. Almost half of these empirical studies were from biological control systems in which the ultimate goal is long-term host suppression. Therefore an extrapolation to the equilibrium situation was implicit in many of these studies. We then present the results of simple models to demonstrate why short-term experiments may bear no relationship to the outcome for the system at equilibrium. Finally, we compare the difference in predictions from the theoretical assumption of a closed system with only 3 interacting species to the predictions for a more realistic system with immigration or alternate resources for the consumers.

A SURVEY OF EMPIRICAL STUDIES

To examine the time scales over which IGP is quantified empirically, we surveyed papers in online, digitally available journals through the University of California Berkeley library with "intraguild pre*" in the title. We restricted this search to years since 1989 when G. Polis and colleagues published their influential *Annual Review of Ecology and Systematics* article (Polis et al. 1989). This search, while not exhaustive, provides a representative sample of recent empirical studies of IGP. Because studies examining biological control systems were most likely to quantify the basal resource density, we added eight studies specifically examining the effect of IGP on the basal resource that did not match our original search criteria.

Our search produced a total of 40 empirical studies of IGP (see Appendix). Using the identities of the IG predator and IG prey, we estimated generation times for each species. Of these experiments, 34 (85%) had durations shorter than the generation time of the IG predator while 29 (73%) were shorter than the generation time of the IG prey (Fig. 1).

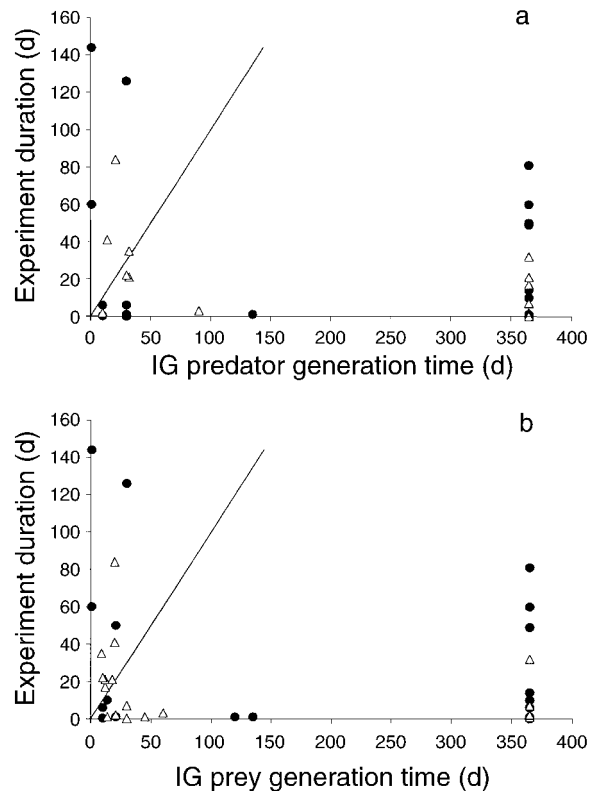


FIG. 1. Duration of intraguild predation experiments as a function of estimated generation time of the (a) IG predator and (b) IG prey. Studies shown as triangles are specifically designed to examine IGP in biological control communities.

Of the 40 studies, 17 specifically examined IGP in biological-control communities (Fig. 1), and 12 of the biological control studies also quantified the effect of IGP on the shared resource. Of the 17 biocontrol studies, 14 (82%) were shorter than the IG predator generation time while 10 (59%) were shorter than the IG prey generation time (Fig. 1). Only two studies quantified the rate of intraguild predation at multiple densities of the shared resource.

This brief survey suggests that empirical IGP studies tend to measure short-term predatory responses (e.g., consumption rate), and even studies designed to make predictions about the effects of IGP in biological control systems are often not designed to capture information about IG predator and IG prey fitness (e.g., population growth rate). Immigration is notoriously difficult to measure and rarely is quantifiable in real systems (Cooper et al. 1998, Rosenheim 2001). However, alternate resources often are available to biological control agents (Evans and England 1996) and produce a similar influx of individuals. In the following sections, we use IGP theory to demonstrate the importance of quantifying fitness effects and the effects of immigration/alternate resource use for long-term predictions about resource density.

SHORT-TERM VS. LONG-TERM PREDICTIONS OF MODELS

Holt and Polis (1997) presented several specific formulations of their general model of intraguild predation. The equations for a simplified version of their model are as follows.

Model 1:

Basal resource: $\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - a_p RP - a_Q RQ$

IG prey: $\frac{dP}{dt} = c_p a_p RP - a_{Q2} PQ - d_p P$

IG predator: $\frac{dQ}{dt} = c_Q a_Q RQ + c_{Q2} a_{Q2} PQ - d_Q Q$

where R is the basal resource, P is the IG prey, and Q is the IG predator; r and K are the intrinsic population growth rate and carrying capacity of the basal resource; a_p and a_Q are attack rates of IG prey and IG predator, respectively, on the basal resource, and a_{Q2} is the attack rate of the IG predator on the IG prey; c_p and c_Q are conversion efficiencies of IG prey and IG predator, respectively, from attacks on the basal resource, and c_{Q2} is the IG predator conversion efficiency from attacks on IG prey; and d_p and d_Q are IG prey and IG predator background death rates.

As we showed in the preceding section, the majority of experiments examining IGP span less than a generation of the IG prey and IG predator. The equations representing these short-term experiments can be reduced to the following.

Model 2:

Basal resource: $\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - a_p RP - a_Q RQ$

IG prey: $\frac{dP}{dt} = -a_{Q2} PQ$

where the density of the IG predator is constant, and the density of the IG prey is only decreased through intraguild predation. This formulation also assumes that experiments are sufficiently short such that IG predator and IG prey mortality due to other sources is unimportant.

Short-term results depend only on attack rates and experimental predator densities

In short-term experiments, which are essentially feeding trials, the effects of the IG predator and IG prey species depend on their experimentally determined densities (and the experimental density of the basal resource), which are often chosen arbitrarily. In addition, their effects depend on the functional response of each (which in this simple model involves just attack rates) and not on conversion efficiency (see Model 2). Fig. 2a shows the density of the basal resource if the experiment described by Model 2 is run for two days, as a function of the density of the IG

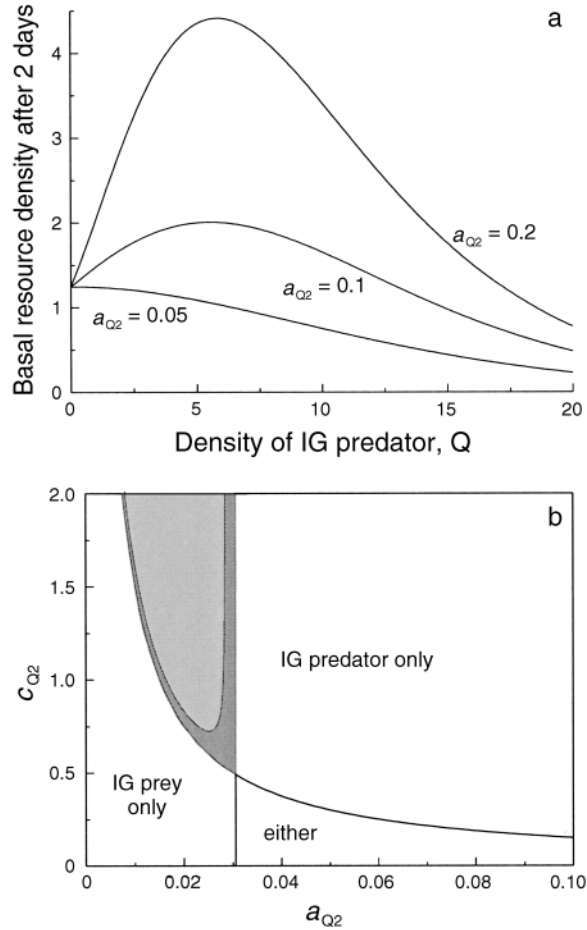


FIG. 2. The interaction between attack rates and conversion efficiencies. (a) Basal resource density after two days of a short-term experiment (Model 2) for three attack rates of the IG predator on the IG prey (a_{Q2}); $r = 1$, $K = 100$, $a_p = 0.2$, $a_Q = 0.1$, $R(0) = 10$, $P(0) = 10$. (b) Long-term outcome of Model 1, in terms of IG predator attack rate on IG prey (a_{Q2}) and conversion efficiency (c_{Q2}). The IG prey invades only to the left of the prey invasion boundary (vertical line). The curved line marks the predator invasion boundary; the IG predator invades only above this boundary. The IG predator and prey coexist only in the shaded region. The three-species equilibrium (IG prey, IG predator, and basal resource) is stable only in the dark shaded region (region determined through standard local stability analysis and confirmed through numerical simulations); in the light shaded region the three species persist in a stable limit cycle (determined through numerical simulations). In the “IG prey only” region, the IG prey persists alone with the resource. In the “IG predator only” region, the IG predator persists with the resource. In the region labeled “either,” the IG predator or the IG prey species prevails, but the outcome depends on initial conditions. Parameter values are the same as in (a) and, additionally, $c_p = 1$, $c_Q = 0.5$, $d_p = d_Q = 0.1$.

predator, Q , for three different values of a_{Q2} , the attack rate of the IG predator on the IG prey. For this illustration, we have chosen the attack rate of the IG prey on the basal resource to be twice that of the IG predator. Without the IG predator ($Q = 0$), the IG prey on its

own can suppress the basal resource density to about 1.25. If a relatively low density of the IG predator is introduced (e.g., $Q = 5$), we would conclude that the IG predator interferes with control of the basal resource (leading to densities greater than those at $Q = 0$) for all but very low values of a_{Q2} . However, at high IG predator densities (e.g., $Q = 15$), we would conclude that adding the IG predator enhances basal resource control for all but very high values of a_{Q2} .

A particular interest for practitioners of biological control is whether the effects of two predators involved in controlling a shared resource will be additive, sub-additive, or strongly interfering in suppressing the basal resource. From our simulation of a two-day experimental study (Fig. 2a), we would conclude that the IG predator, at low density ($Q = 5$), would interfere in control of the basal resource unless it had a very low attack rate on the IG prey. In contrast, if we introduced a high density of the IG predator ($Q = 20$) into our experiment, we would conclude that the species provide additive control.

But what is the relationship between short experiments and IGP equilibrium predictions?

Attack rates alone are insufficient to make predictions about long-term suppression

Model 2, examined in the previous section, reflects short-term experimental studies and includes only attack rates of the IG prey and IG predator. A predator's attack rate is simply the fraction of available prey that a predator can find and eat per unit time. This can give an indication of the predator's effectiveness at inflicting mortality on its resource. This may be useful for short-term control, or biocontrol programs involving inundative release of predators. Attack rates alone, however, tell only part of the story about long-term suppression of the basal resource. An equally important factor for long-term suppression is the predator's conversion efficiency, i.e., how many new predators are produced from each unit of resource ingested by that predator.

In this long-term intraguild predation model (Model 1), the equilibrium density of the basal resource and the IG prey is

$$R^*|_p = \frac{1}{c_p a_p T_p}$$

denoting the density of R at the equilibrium with only the IG prey, i.e., without the IG predator. $T_p = 1/d_p$ is the average lifespan of the IG prey. Similarly, the basal resource equilibrium with the IG predator is

$$R^*|_Q = \frac{1}{c_Q a_Q T_Q}$$

denoting the density of R at the equilibrium with only the IG predator, i.e., without the IG prey, where $T_Q = 1/d_Q$, is the IG predator's average lifespan. Thus, for long-term control of the basal resource, predator attack

rates, conversion efficiencies, and longevities are interchangeable.

A predator that kills or consumes prey at a high rate may effectively suppress the prey in a short-term feeding trial, but if that predator is short-lived or inefficient at converting prey into new predators, then that species may be ineffective for long-term control. Conclusions about long-term control cannot be drawn solely from short-term experiments that measure only attack rates. If the IG predator is long-lived and/or has high conversion efficiency, it may be the better species at long-term control of the basal resource, even if the results of short-term experiments (e.g., Fig. 2a) suggest that it disrupts control.

Attack rates alone are insufficient to make predictions about long-term coexistence

Similarly, a quantification of attack rates alone will not necessarily tell us whether the IG prey and IG predator will be able to coexist on the basal resource. In a closed system, a necessary condition for coexistence is that the IG prey on its own must be more efficient than the IG predator at suppressing the density of the basal resource. However, this is not a sufficient condition, and the actual outcome depends on a number of other factors, including the attack rate and conversion efficiency of the IG predator on the IG prey. Fig. 2b shows the long-term outcome of intraguild predation, for a situation in which the equilibrium density of the basal resource set by the IG prey is one-quarter that set by the IG predator. In the long term, depending on the values of a_{Q2} and c_{Q2} , any outcome is possible, including exclusion of the IG prey by the IG predator, exclusion of the IG predator by the IG prey, and a region in which the outcome depends on the initial conditions (Fig. 2b). Coexistence of the IG prey and IG predator on the basal resource occurs only in a narrow range of parameters in which the IG predator has a limited attack rate on the IG prey, but high conversion efficiency. Coexistence or competitive exclusion also is affected by basal resource productivity (Holt and Polis 1997, Borer et al. 2003).

In the shaded region of Fig. 2b, where the IG prey and IG predator coexist, the resulting equilibrium of the basal resource is intermediate between the density set by the IG prey and that set by the IG predator. This is a general result: in a closed system, in the absence of other forms of intraspecific interference, whenever the IG prey and IG predator coexist, the equilibrium density of the basal resource is higher than the density that could be achieved by the IG prey on its own. Thus, the presence of the IG predator always interferes with control of the basal resource. However, as we will see in the next section, this is true only in a closed system.

Open systems change everything

The model of long-term intraguild predation above (Model 1) assumes that intraguild predation takes place

in a closed three-species system. The IG prey feeds only on the basal resource, and the IG predator feeds on both the basal resource and the IG prey and nothing else. No individuals disperse into or out of the local area. In real systems, such as biological control communities, complete specialization is rare (Godfray 1994, Evans and England 1996, Rosenheim 2001, vanRijn et al. 2002), which means that one or both predators may also consume other resources. In addition, in one particularly well-studied example of intraguild predation in an agricultural system (Rosenheim 2001), the IG prey is believed to persist only through immigration from external source populations outside the system.

To examine the role of immigration, we investigate a very simple modification of Model 1, with the addition of immigrants.

Model 2a:

$$\begin{aligned} \text{Basal resource: } \frac{dR}{dt} &= rR \left(1 - \frac{R}{K}\right) - a_p RP - a_Q RQ \\ \text{IG prey: } \frac{dP}{dt} &= c_p a_p RP - a_{Q2} PQ - d_p P + I_p \\ \text{IG predator: } \frac{dQ}{dt} &= c_Q a_Q RQ + c_{Q2} a_{Q2} PQ \\ &\quad - d_Q Q + I_Q \end{aligned}$$

where I_p and I_Q represent inputs of IG prey and IG predator, respectively, from outside the system. This could represent repeated releases of biological control agents, constant immigration from outside the local area, or increased population growth rate of each species caused by consumption of an alternate resource which is not modeled explicitly.

Inputs of either the IG predator or IG prey can alter our predictions about coexistence. Any extra input of the IG predator, $I_Q > 0$, gives the IG predator an additional advantage, narrowing the region over which the IG prey can persist. An input of the IG prey, $I_p > 0$, gives an extra advantage to the IG prey. With $I_p > 0$ the IG prey can persist and coexist with the IG predator across a broader range of parameter values than was possible in the absence of this subsidy. For example, with enough IG prey input, the IG prey and IG predator can coexist even if the IG predator is superior at suppressing the basal resource.

Inputs of the IG predator and IG prey can also alter our predictions about the equilibrium density of the basal resource. When the IG predator is superior at suppressing the basal resource, the addition of the IG predator can enhance, rather than disrupt, control of the basal resource. For example, Fig. 3a shows the effect of increasing the input of IG prey on the equilibrium density of the basal resource when the attack rate of the IG predator on the basal resource is twice that of the IG prey (with $c_p = c_Q$ and $d_p = d_Q$). When $I_p = 0$, the equilibrium density of the basal resource

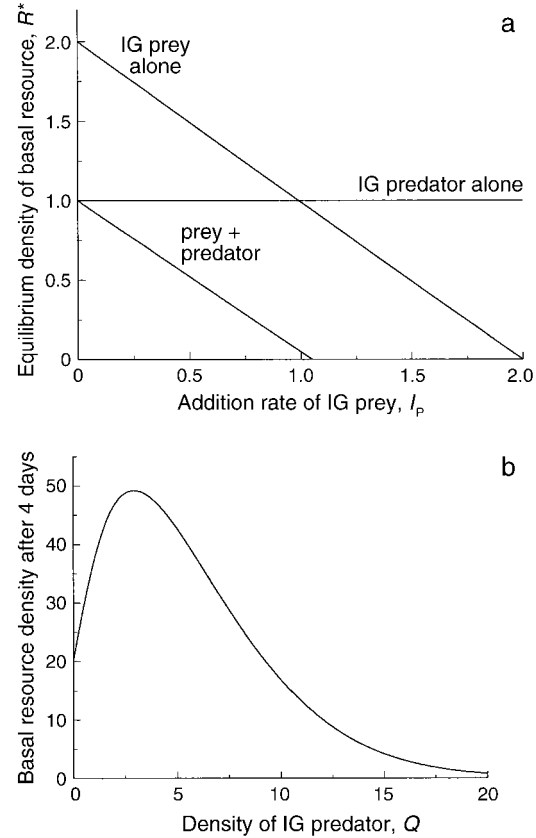


FIG. 3. Immigration has important dynamic effects. (a) Effects of increasing the rate of addition of IG prey from outside the system, I_p , on the equilibrium resource density, R^* , for the IG prey alone, the IG predator alone, and IG prey and IG predator coexisting; $r = 1$, $K = 100$, $a_p = 0.05$, $a_Q = 0.1$, $c_p = c_Q = c_{Q2} = 1$, $d_p = d_Q = 0.1$, $a_{Q2} = 0.2$, and $I_Q = 0$. (b) The short-term outcome (after four days) for basal resource density caused by varying initial IG predator density (Model 2), for the same parameters as in (a). The short-term experiment is in a closed system, with no immigration. Parameter values are the same as in (a) and, additionally, $R(0) = 100$, $P(0) = 20$.

set by the IG predator is half that set by the IG prey, and the two predators cannot coexist. However, for moderate values of $I_p > 0$, the two predators can coexist, and the resulting equilibrium density of the basal resource is lower than that set by either guild member on its own. Thus, in this situation, addition of either the IG predator or IG prey reduces the ultimate density of the resource. With high IG prey subsidies (above about 1.1 in Fig. 3a), the basal resource is driven extinct, the IG predator persists through attacks on the IG prey, and the IG prey persists through constant subsidies. With only the IG prey present, the equilibrium density of the basal resource decreases linearly with increasing I_p .

Short-term experiments of such a system could again be misleading. For example, a subsidy for the IG predator will cause a decrease in the equilibrium of the

basal resource, below that which would be expected based on attack rate alone. Thus, short-term experiments that measure only attack rate could underestimate the impact of an IG predator species on the basal resource, if the IG predator's population were subsidized from outside the system. Depending on the densities of IG prey and IG predators examined in an experiment, short-term feeding trials may suggest that the IG predator would interfere with control (e.g., low densities of the IG predator in Fig. 3b), while at equilibrium it will, in fact, enhance control.

DISCUSSION

We use an intentionally simple model to make the point that empirically measured attack rates or short-term feeding preferences alone can be misleading when making long-term predictions about species abundances in systems with intraguild predation. While the general problem of a mismatch between short- and long-term model predictions has received increasing attention in the recent literature (Brown et al. 2001, Hastings 2004), it is worth reiterating this point in a specifically applied context, given that our brief review of this empirical literature reveals that very short-term experiments are currently the norm in the field and provide the foundation for many policy decisions. With this simple model we underline the importance of empirically quantifying IG predator and IG prey fitness effects.

The results of the current study have direct relevance to the implementation of biological control in systems with IGP. In spite of calls for multi-generational studies of biological control agents (Brodeur and Rosenheim 2000), recent guidelines for biological control programs in the European Union stress only short-term tests of feeding preferences (van Lenteren et al. 2003). While experiments long enough to quantify IG predator and IG prey progeny production (i.e., conversion efficiency) will be more expensive than short-term consumption estimates, a few longer-term experiments would provide important model parameter estimates for biological control programs. Combined with information from less expensive and time-consuming short-term studies, these multi-generation estimates will produce far better predictions about the long-term success of biological control. The results of our simple models demonstrate why investment in a few strategic, though more costly, multigenerational studies will lead to far better predictions about the efficacy of potential biological control communities.

In addition, although knowledge about IG predator and IG prey conversion efficiency is crucial for long-term predictions, we note that in some cases, short-term experiments may provide a reasonable estimate of long-term dynamics. In particular, parasitoids, commonly used as natural enemies in biological control, are often efficient at converting resources into progeny (Godfray 1994). Juvenile mortality and host-feeding,

in which attacks on hosts do not translate directly into progeny, can cause parasitoid population growth rate to fall short of attack rates (Collier 1995, Mills and Getz 1996, Murdoch et al. 1997). However, given high juvenile survival and low host-feeding rates, the high biological efficiency of parasitoids means that short-term host-parasitoid experiments examining intraguild predation may provide a sufficient estimate of long-term system dynamics for predicting biological control efficacy.

An important issue that we did not examine here is the effect of nonlinear functional responses (Soluk 1993, Ives et al. 1999). However, an earlier study of IGP has shown that saturating functional responses can alter IGP theoretical predictions (Revilla 2002). Thus, even if multi-generation experiments are conducted to quantify conversion efficiencies of both the IG predator and IG prey, nonlinear functional responses may cause these empirical results to hold only for the resource densities examined in the experiment. In systems where non-linear functional responses are known or suspected for a species, empirical work must be done across a broad range of resource density or resource productivity.

We illustrate that systems with repeated releases of, immigration of, or alternate resources for, the IG predator or IG prey are dynamically different than the closed systems modeled in the original IGP formulation. In systems with immigration or alternate resources, we have used simple models to clearly show that the equilibrium outcome for the system depends most strongly on the rate of external subsidies. Immigration can alter both community dynamics and community composition in real and model systems (Levins and Culver 1971, Manne et al. 1998, Holyoak 2000, Holt 2002). In the context of these recent metacommunity studies, it is not surprising that recruitment from external sources can dramatically alter our predictions about systems with IGP, as well. Important for biological control is that immigration rates and alternate resources can completely alter predictions about short-term and equilibrium densities of the basal resource compared to closed-system models. Without immigration rate and alternate resource use estimates in systems with IGP, the importance of IGP in determining community dynamics will be impossible to assess.

With the explosion of empirical investigations into the role of IGP in many real ecological systems, we have used simple models to emphasize the necessity of multi-generational studies for making quantitative predictions about systems with IGP. Attack rates, conversion efficiencies, and IG predator and IG prey immigration rates must be quantified for a long-term understanding of the role of IGP in field systems. More generally, the results of the current models demonstrate that assessments of community dynamics must be based on appropriate parameter values and an awareness of the role of equilibria in the model predictions.

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LITERATURE CITED

- Borer, E. T., C. J. Briggs, W. W. Murdoch, and S. L. Swarbrick. 2003. Testing intraguild predation theory in a field system: does numerical dominance shift along a gradient of productivity? *Ecology Letters* **6**:929–935.
- Brodeur, J., and J. A. Rosenheim. 2000. Intraguild interactions in aphid parasitoids. *Entomologia Experimentalis Et Applicata* **97**:93–108.
- Brown, J. H., T. G. Whitham, S. K. M. Ernest, and C. A. Gehring. 2001. Complex species interactions and the dynamics of ecological systems: long-term experiments. *Science* **293**:643–650.
- Collier, T. R. 1995. Host feeding, egg maturation, resorption, and longevity in the parasitoid *Aphytis melinus* (Hymenoptera: Aphelinidae). *Annals of the Entomological Society of America* **88**:206–214.
- Cooper, S. D., S. Diehl, K. Kratz, and O. Sarnelle. 1998. Implications of scale for patterns and processes in stream ecology. *Australian Journal of Ecology* **23**:27–40.
- Evans, E. W., and S. England. 1996. Indirect interactions in biological control of insects: pests and natural enemies in alfalfa. *Ecological Applications* **6**:920–930.
- Godfray, H. C. J. 1994. *Parasitoids: behavioral and evolutionary ecology*. Princeton University Press, Princeton, New Jersey, USA.
- Hastings, A. 2004. Transients: the key to long-term ecological understanding? *Trends in Ecology and Evolution* **19**:39–45.
- Holt, R. D. 2002. Food webs in space: on the interplay of dynamic instability and spatial processes. *Ecological Research* **17**:261–273.
- Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. *American Naturalist* **149**:745–764.
- Holyoak, M. 2000. Habitat subdivision causes changes in food web structure. *Ecology Letters* **3**:509–515.
- Ives, A. R., S. S. Schooler, V. J. Jagar, S. E. Knutson, M. Grbic, and W. H. Settle. 1999. Variability and parasitoid foraging efficiency: a case study of pea aphids and *Aphidius ervi*. *American Naturalist* **154**:652–673.
- Levins, R., and D. Culver. 1971. Regional coexistence of species and competition between rare species (mathematical model/habitable patches). *Proceedings of the National Academy of Sciences (USA)* **68**:1246–1248.
- MacNeil, C., E. Bigsby, J. T. A. Dick, M. J. Hatcher, and A. M. Dunn. 2003. Differential physico-chemical tolerances and intraguild predation among native and invasive amphipods (Crustacea); a field study. *Archiv Fur Hydrobiologie* **156**:165–179.
- Manne, L. L., S. L. Pimm, J. M. Diamond, and T. M. Reed. 1998. The form of the curves: a direct evaluation of MacArthur and Wilson's classic theory. *Journal of Animal Ecology* **67**:784–794.
- Mills, N. J., and W. M. Getz. 1996. Modelling the biological control of insect pests: a review of host-parasitoid models. *Ecological Modelling* **92**:121–143.
- Murdoch, W. W., C. J. Briggs, and R. M. Nisbet. 1997. Dynamical effects of host size- and parasitoid state-dependent attacks by parasitoids. *Journal of Animal Ecology* **66**:542–556.
- 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. 1998. Higher-order predators and the regulation of insect herbivore populations. *Annual Review of Entomology* **43**:421–447.
- Rosenheim, J. A. 2001. Source-sink dynamics for a generalist insect predator in habitats with strong higher-order predation. *Ecological Monographs* **71**:93–116.
- Rosenheim, J. A., H. K. Kaya, L. E. Ehler, J. J. Marois, and B. A. Jaffee. 1995. Intraguild predation among biological control agents: theory and evidence. *Biological Control* **5**:303–335.
- Soluk, D. A. 1993. Multiple predator effects: predicting combined functional response of stream fish and invertebrate predators. *Ecology* **74**:219–225.
- van Lenteren, J. C., et al. 2003. Environmental risk assessment of exotic natural enemies used in inundative biological control. *Biocontrol* **48**:3–38.
- vanRijn, P. C. J., Y. M. vanHouten, and M. W. Sabelis. 2002. How plants benefit from providing food to predators even when it is also edible to herbivores. *Ecology* **83**:2664–2679.
- Venzon, M., A. Janssen, and M. W. Sabelis. 2001. Prey preference, intraguild predation and population dynamics of an arthropod food web on plants. *Experimental and Applied Acarology* **25**:785–808.

APPENDIX

A summary of the experiments used to examine intraguild predation is presented in ESA's Electronic Data Archive: *Ecological Archives* A015-030-A1.