

Intraguild predation in biological control and conservation biology

Christine B. Müller^{a,*} and Jacques Brodeur^b

^a *Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK*

^b *Centre de recherche en horticulture, Département de phytologie, Université Laval, Sainte-Foy, Que., Canada G1K 7P4*

Received 2 November 2001; accepted 27 April 2002

Abstract

Intraguild predation has become a major research topic in biological control and conservation ecology. Theoretical studies on intraguild predation have advanced in food web ecology and point towards basal resources being an important predictor of the outcome and the stability of intraguild interactions. Here we introduce the concept of intraguild predation and highlight the complexity of ecological interactions that may arise in natural multi-predator systems due to species diversity and patterns of abundance. We discuss the application of intraguild predation in biological control programs and conservation management, and suggest that productivity gradients should be considered in future experiments.

© 2002 Elsevier Science (USA). All rights reserved.

Keywords: Biological control; Conservation ecology; Hyperpredation; Intraguild predation; Mesopredator release; Omnivory; Productivity

1. Introduction

Most communities include an array of top consumers, none of which may be strictly monophagous, but many of which may be competing for the same prey (Sih et al., 1985). It is therefore critical to understand the effects that multiple predators can have on each other and on their shared prey populations. In concert with the diversity of predators, a variety of direct and indirect ecological effects can be expected (Sih et al., 1998). In particular, intraguild predation occurs when two predator species compete for the same prey and one of them also feeds upon its competitor (Polis et al., 1989). As a consequence, intraguild predation combines two important structuring forces in ecological communities: competition and predation (Polis and Holt, 1992; Polis and Winemiller, 1996), and may generate a diversity of indirect effects among co-occurring species.

Intraguild predation has long been considered in basic food-web ecology where it is generally referred to as 'omnivory,' a term that applies more widely to species that feed on more than one trophic level (Pimm and Lawton, 1978). Although theoretically expected to be

rare (Pimm et al., 1991), omnivory appears to be common in many natural communities (Coll and Guershon, 2002; Person et al., 1996; Polis et al., 1989), indicating that food webs are not ordered in strict trophic levels because most species eat more than one kind of food (Polis and Strong, 1996). A number of models investigating the role of omnivory on the structure of communities have been developed (Holt and Polis, 1997; May and Hassell, 1981; Pimm, 1991; Pimm and Lawton, 1978; Rosenzweig, 1977), but it remains controversial whether and under what ecological conditions omnivory (or intraguild predation) has a stabilizing effect on community structure (Brodeur and Rosenheim, 2000; Coll and Guershon, 2002; McCann and Hastings, 1997; McCann et al., 1998; Rosenheim, 1998).

The prey resource is the template that influences interactions between intermediate and top predators. Most theoretical models that address intraguild predation are based on equilibrium models. However, more recently there has been an increasing awareness that biological control occurs in highly non-equilibrium systems that show strong transitory dynamics (Fenton et al., 2001; Holt and Lawton, 1993). Holt and Polis (1997) theoretically explored the ecological conditions that determine the magnitude and stability of intraguild predation. Because intraguild predation is closely linked to other kinds of

* Corresponding author. Fax: +807-483-8837.

E-mail address: christine.mueller@ioz.ac.uk (C.B. Müller).

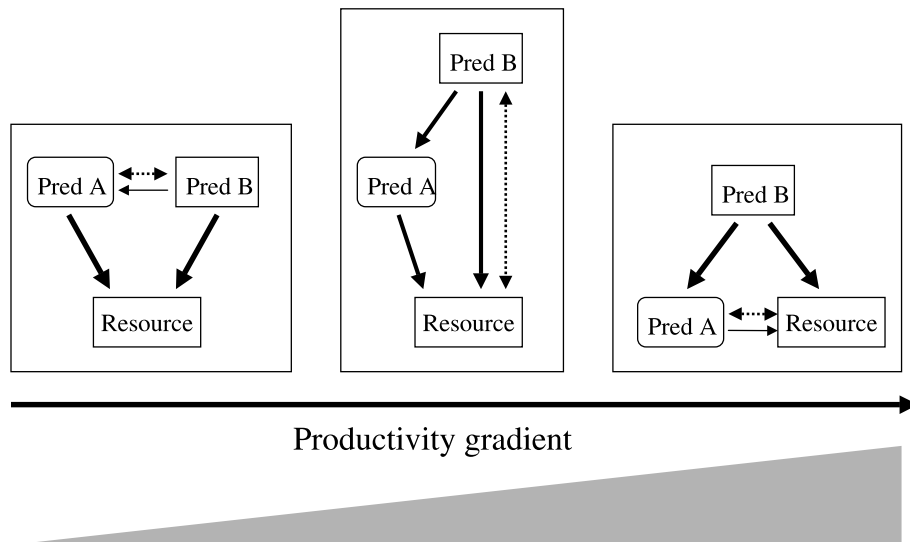


Fig. 1. Transitions from exploitation competition (i.e., two consumers share and compete for the same resource) to intraguild predation (i.e., two consumers share and compete for the same resource but also engage in direct feeding relationship) and apparent competition (i.e., two resource species share the same consumer). The intermediate predator (or 'mesopredator') A is switching trophic position along an increasing productivity gradient. Solid, thick arrows are trophic interactions, broken arrows are indirect effects, and thin, solid arrows are interactions that loose significance.

indirect interactions, such as exploitative competition, trophic cascades and apparent competition, transitions between those related interactions may take place as a result of changes in either population densities or species specific traits (Fig. 1; Abrams et al., 1996). It has been suggested that such transitions may depend upon the productivity of the system, with exploitation competition (i.e., interaction via the shared resource; see also Pérez-Lachaud et al., 2001) being more significant in poor systems, apparent competition (i.e., interaction via a shared predator; see also Hoogendoorn and Heimpel, 2001) in rich systems, and intraguild predation in systems of intermediate productivity (Holt and Polis, 1997; Fig. 1). For intraguild predation to be stable, the intermediate predator has to be the better competitor for the shared resource than the top predator (Holt and Polis, 1997; T. Mitsunaga and E. Yano, unpublished data). It follows that when resources become scarce the top predator may be eliminated from the system by losing out in exploitative competition for the prey resource. In this case, coexistence is only possible when there is resource or niche partitioning between the two predators. As resources become abundant, the intermediate predator may lose out through predator-mediated apparent competition with its own prey. To our knowledge, this argument has not yet been supported with empirical evidence in terrestrial natural or managed ecosystems.

Intraguild predation is not only driven by prey species abundance (Colfer and Rosenheim, 2001; Lucas et al., 1998), but has consequences for the abundance of the prey species. The effects of one predator on another may result in enhanced risk of predation for the prey through additive or synergistic actions of predators (Ferguson and Stiling, 1996; Losey and Denno,

1998a,b,c; Mesquita et al., 1997). Alternatively, interactions between natural enemies may release prey from predation when the trophic or behavioural interactions between predators dominate (Cisneros and Rosenheim, 1997; Ferguson and Stiling, 1996; Lucas et al., 1998; Rosenheim et al., 1993; Taylor et al., 1998). As various outcomes for the prey resource arise from intraguild predation, it may depend on the identities of the species that interact; this in turn makes the outcome of this indirect interaction less predictable.

Intraguild interactions and their consequences for prey population dynamics and community structure have become a major topic in applied fields. Intraguild predation represents a possible threat to successful biological control (Rosenheim, 1998; Rosenheim et al., 1995), but may be desirable for the conservation of natural communities (Soulé et al., 1988; Zavaleta et al., 2001). In the following we will use aphid systems and the associated natural enemies to demonstrate the complications arising from indirect community effects. Such complications are a consequence of species richness and environmental variability that are commonly found in natural communities. Moreover, we will describe and contrast the role of intraguild predation in biological control and conservation management.

2. Natural aphid communities

For the trophic cascade effect of intraguild predation to be biologically significant, the interaction between the two predators and the prey has to be strong. An intraguild predation effect is therefore most likely to occur in relatively simple assemblages such as aquatic food

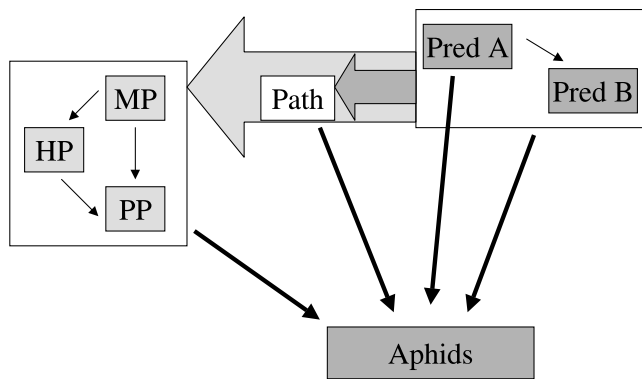


Fig. 2. Possible feeding interactions within an assemblage of aphids and their associated natural enemies. Note that depending on the definition of 'guild,' intraguild predation will be observed in different places. PP, primary parasitoid; HP, hyperparasitoid; MP, mummy parasitoid; Path, aphid specific pathogenic fungi; Pred A, adult predator; Pred B, larval predator, black arrows are possible trophic interactions, and grey arrows depict possible 'priority effects' for consumption.

chains or agro-environments (Leibold, 1989; Polis, 1999; Polis et al., 2000; Schmitz et al., 2000) that have relatively low species richness but high species abundance. Natural communities in terrestrial settings are more complex networks than community modules or simple trophic chains and represent a challenge for the development of theory on community interactions as dy-

namical switching between trophic levels may be common (Polis and Strong, 1996; Simberloff and Stiling, 1996a,b).

Like most invertebrate assemblages, aphid communities are extremely species-rich and many different kinds of interaction are possible among parasitoids, predators and aphid-specific pathogens (Brodeur and Rosenheim, 2000; Müller and Godfray, 1999a; Müller et al., 1999; Müller et al., in prep.). Assuming all organisms that feed on aphids belong to the same guild (following Rosenheim et al., 1995), most natural enemies in this system interact asymmetrically because of differences in body size, feeding strategies and priority effects. The latter refers to the sequence and timing of attack, larval developmental times and the time it takes to kill the prey, which may all differ among the different classes of natural enemies. Insect predators appear to be the superior group of natural enemies, also consuming infected and parasitized aphids (Fig. 2; see also Meyhöfer, 2001).

Comparing the three groups of natural enemies, the highest degree of shared prey was found among predators and the least resource overlap among parasitoids (Müller et al., in prep.). This is reflected in experimental results, demonstrating strong apparent competition among aphids via shared predators (Müller and Godfray, 1997, 1999b), but providing inconclusive results for both parasitoids (Morris et al., 2001; Rott et al., 1998) and pathogens (Pope et al., 2002). Predators that

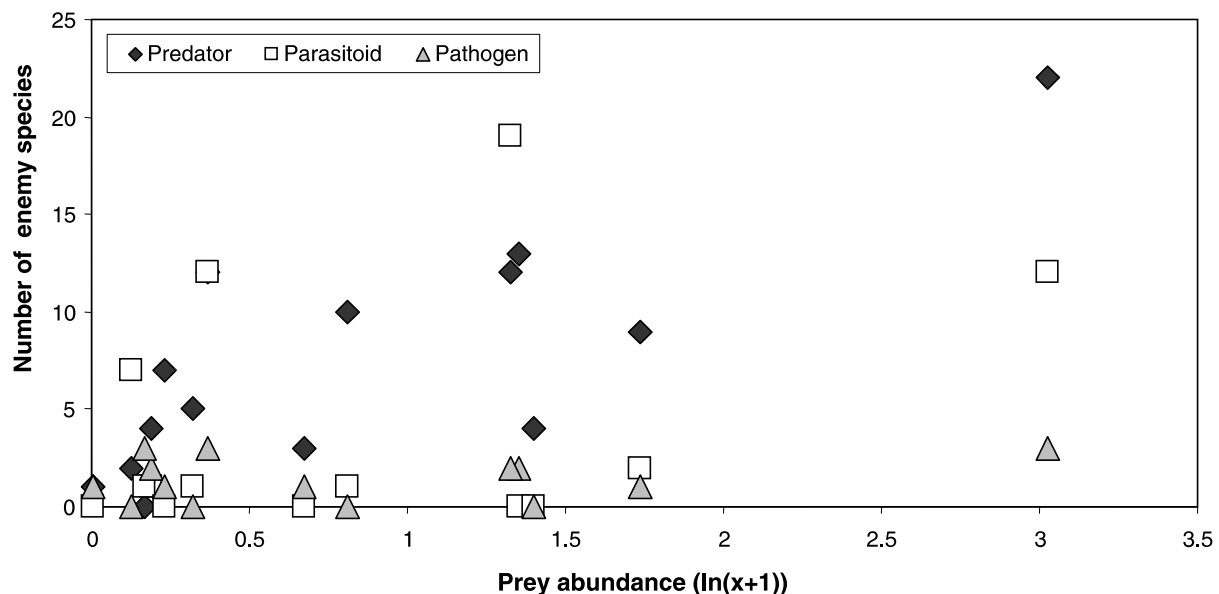


Fig. 3. The relationship between aphid abundance (expressed as aphids per m^2 and averaged over the whole season of 1996; abundance is $\ln(x+1)$ -transformed) and the number of species of predators (black symbol), parasitoids (white symbol), and pathogens (grey symbol) associated with the respective aphid prey or host species. The correlation between prey abundance and number of species in each natural enemy class was 0.80, 0.37, and 0.25 for predator, parasitoid, and pathogen species, respectively. The data are derived from a long-term study on aphid and natural enemy community structure in a natural, abandoned field in Silwood Park, UK. Aphid and parasitoid abundance for all species is recorded by counts at two-weekly intervals between April and October since 1994 to construct fully quantified food webs. Since 1996, the abundance of fungal pathogens is also recorded and arthropod predator abundance has been quantified in 1996. For further details on the study site and the sampling scheme see Müller et al. (1999).

aggregate in aphid colonies will consume parasitized aphids or aphid mummies (Müller and Godfray, 1997). It has been suggested that aphid parasitoids avoid patches in which secondary parasitoids (Höller et al., 1993) and predators (Taylor et al., 1998) are foraging. The latter is a likely response to the risk of intraguild predation because parasitoid larvae restricted to the host during their development are an easily exploitable prey for aphidophagous insects (Colfer and Rosenheim, 2001; Ferguson and Stiling, 1997; Frazer and Gilbert, 1976; Wheeler et al., 1968).

For strong effects by intraguild predation to occur, the density of aggregating natural enemies should depend on prey abundance. However, for aphid parasitoids this may not always be the case (Müller and Godfray, 1998) and may strongly depend on the spatial scale investigated (Schooler et al., 1996; van Veen et al., 2002). Fig. 3 shows that the number of species within different classes of natural enemies associated with given prey aphid species has no strong relationship with prey abundance except in the case of predators. This may explain why predators can drive indirect interactions such as apparent competition while evidence remains weak for parasitoids and pathogens. Other classes of natural enemies may be either too species poor (pathogens) or too specialized (parasitoids). Furthermore, if the highest number of predator species is found on the most abundant prey resource, any strong interaction between predator and prey may get diffused through multiple predator effects.

3. Biological control

In their seminal review, Rosenheim et al. (1995) asked whether intraguild predation can be disruptive for biological control, and what is the evidence for it to be a common phenomenon. They use intraguild predation in a broad sense, defining ‘guild’ as all organisms that share a common food resource that is exploited in the same or in different ways. Intraguild predators are thus organisms that compete for the same food resource but have also a direct trophic interaction. Two predators can engage in symmetrical (both feeding on each other) and asymmetrical (A feeding on B but not vice versa) interactions which may change over time due to ontogenetic, size-dependent relationships (Polis and Strong, 1996). Intraguild predation may include both, taxonomically very distant or very close organisms, and this will, to a certain degree, influence predictions for the possible outcome of the interaction. The broad definition of Rosenheim et al. (1995) excludes cannibalism and obligate secondary parasitism, although it does include microorganisms [leading to ‘between kingdom interactions,’ *sensu* Hochberg and Lawton, 1990] as well as facultative hyperparasitoids.

The evidence reviewed by Rosenheim et al. (1995) points towards biological control systems involving nematode and arthropod pest species being most affected by intraguild predation, and control of plant diseases being least affected by interactions between plant pathogen antagonists. Intraguild predation will more often be disruptive when predators (mites, insects, and fish) are involved and more unpredictable in terms of control of the target pest species when pathogens or facultative hyperparasitoids interact with primary parasitoids (Rosenheim et al., 1995). The latter is perhaps not surprising because it is difficult to determine whether competition does actually dominate parasitoid assemblages (Hawkins, 2000). Rosenheim et al. (1995) conclude that because communities are often complex networks of interactions and because laboratory experiments deprive test organisms of alternative food sources and reduce spatial distribution, there is a need for more information from field experiments and long-term community-level studies.

Although studies on intraguild predation have their traditional focus on the action of natural enemies (top-down), research on biological control has started to acknowledge the importance of resource-based factors (bottom-up). For example, in a review of 68 life tables used to analyze herbivore control by natural enemies in natural and agricultural settings, Hawkins et al. (1999) found that top-down forces in natural and agricultural systems differ and therefore concluded that biological control of pests cannot be equalized with ‘natural control’ of herbivores. Introduced parasitoids appear to be more likely to successfully control herbivores in simplified, managed agroecosystems, which are dominated by exotic species of plants and herbivores, whereas predators may dominate in herbivore control within natural systems. They suggested that this may reflect differences in food web complexity which in turn could be linked to differences in resource abundance and productivity between the two systems. For intraguild interactions in particular, it has also been argued that spatial settings and prey densities (i.e., resource abundance) are strong determinants of the resulting possibility of prey release (Lucas et al., 1998; Raymond et al., 2000; Rosenheim, 2001).

In contrast to Rosenheim et al.’s study (1995), another major review of natural enemy interactions across agricultural ecosystems by Sunderland et al. (1997) avoided the term intraguild predation, possibly because of their more restricted definition of a guild as a group of organisms exploiting the same resources in the same way (after Root, 1967). Such a definition clearly separates predators, parasitoids and pathogens into different trophic guilds. In their review they used the term ‘hyperpredation’ as the condition whereby predators include other predators amongst their prey (this expression is a derivate of ‘hyperparasitism’ which

refers to one parasitoid attacking another, W. Powell, pers. comm.). Sunderland et al. (1997) further concluded that inter- and intraspecific, agonistic behaviour among predators may be disruptive for biological control. Clearly, intraguild predation relies on the definition of trophic guild which in itself is a useful concept, grouping all species in a community that make use of the same ecological resource. There is a consensus that studies of the biological control of pest arthropods and biological control theory should take into account the possible effects of intraguild predation. Many specific studies have been carried out to test the potentially damaging effects of multiple predators and, in particular, to answer whether only one or multiple enemies should be released to achieve optimal pest control (see Bellows and Hassell, 1999 and references therein).

4. Conservation management

Researchers in conservation ecology are very aware of one effect of intraguild predation that occurs when top predators are removed from a system: mesopredator release (i.e., the intermediate predator becomes the sole consumer of the shared prey) (see Fig. 1; Courchamp et al., 1999; Palomares and Caro, 1999; Soulé et al., 1988). Many cases of this aspect of intraguild predation have been reported. For example, the vulnerable endemic flightless parrot kakapo (*Strigops habroptilus* G.R. Gray) and other endemic bird species on small islands in New Zealand suffer from predation by both rats (*Rattus* spp.) and feral house cats (*Felis catus* L.). Cats are maintained at high population densities by feeding on rats, their main prey. Rats act as mesopredators representing the main prey for cats but also feeding on bird eggs and chicks (Karl and Best, 1982). Without simultaneous removal of both top and intermediate predator, the parrot population is doomed because cat removal would lead to 'mesopredator release,' thereby damaging the parrot population even more severely than with both predators present (Zavaleta et al., 2001). If top predators vanish from a system, as was demonstrated for declining coyote (*Canis latrans* say) populations in Southern California, populations of mesopredators such as raccoons (*Procyon lotor* (Linnaeus)) or feral house cats increased due to the relaxation of intraguild predation and competition, thus becoming a major threat for native bird populations (Crooks and Soulé, 1999; Rogers and Caro, 1998). Similarly, in areas where Iberian lynx (*Felis pardina* (Temminck)), mongoose (*Herpestes ichneumon* (Linnaeus)) and rabbits (*Oryctolagus cuniculus* L.) interact, the removal of lynx results in decreased rabbit abundance because of relaxed intraguild predation and subsequent mesopredator release (Palomares et al., 1994).

Finally, 'hyperpredation' is also used in conservation ecology where it refers to a special case of apparent competition when both predator and alternative prey are introduced into a new habitat simultaneously. The exotic prey population will then inflate the predator population causing strong predation pressures with possible, subsequent extinction of a native prey (Courchamp et al., 2000; Smith and Quin, 1996). Because the exotic prey may not always exploit the native prey as a food source (i.e., no shared prey), the interaction resembles apparent competition rather than intraguild predation.

5. Conclusions

Natural communities are dominated and controlled by top-down and bottom-up forces (Hunter and Price, 1992) and it follows that the interactions within such communities will be under the influence of both forces. Considerable theory on multitrophic species interactions and top-down and bottom-up influences has been developed (Holt et al., 1994; Leibold, 1989, 1996; Power, 1992) but there is still a paucity of good experimental evidence from field studies. By their nature, multi-species experiments are difficult, yet essential, to allow predictions to be made for both biological control and conservation management strategies. Traditionally, the field has been split between research on predation focusing on top-down forces and research on productivity and resource quality focusing on bottom-up effects (Power, 1992). However, it would be desirable that an integrated approach is used for experimental studies on multi-species and multi-level interactions. Habitat productivity influences the relative importance of predation and competition, the two forces in intraguild predation. This has been demonstrated experimentally in a microbial model system (Bohannan and Lenski, 2000) in which two *Escherichia coli* strains (*E. coli* B strain REL607 and REL6584) with differential exploitation and predator resistance traits compete for a shared resource but also share a bacteriophage. As predicted by models, at low productivity the better exploiter excludes the more predator-resistant strain because exploitation is more important. At high productivity, predation becomes relatively more important and the predator-resistant strain will exclude the better competitor. Interestingly, at intermediate productivity the two strains can coexist due to a trade-off between exploitation and predator resistance. This example should prompt field researchers to design experiments that investigate the dynamics of intraguild predation along productivity gradients. The findings of such studies would greatly contribute to achieving a predictive understanding of the potential success and consequences of biological control programs and specific conservation actions.

Biological control and conservation biology tackle similar problems when it comes to understanding the role of multi-predator interactions in the extirpation or maintenance of a 'target' species. On the one hand, biological control adds one or several predators to a pest system and asks which combination damages the prey (pest) population most. Although not always explicitly stated, the idea is to avoid the prey release effect of intraguild predation. On the other hand, conservation research is often preoccupied by the loss of top consumers that can indirectly damage prey populations through mesopredator release. Here intraguild predation is desired because it keeps the mesopredators in check and allows coexistence of more species. Arguably both lines of research deal with somehow artificial (anthropogenic) conditions because many effects are generated by species introductions or extinctions that are intentional or accidental. However, this intervention or forcing of natural systems make biological control and conservation cases useful in the study of large consequences of trophic interactions that would be otherwise difficult to address by controlled field experimentation. Predictably, the two fields of research will interact more strongly in the future because of the growing awareness that introduced biological control agents can also have unwanted effects on non-target, native prey populations (Follett and Duan, 2000; Henneman and Memmott, 2001; Scott and Quimby, 2001; Simberloff and Stiling, 1996a,b).

Quantification of multi-predator interactions and an understanding of the consequences on target prey populations are needed to implement biological control and conservation programs. Our limited but growing ability to predict the responses of interacting species to introduction, removal, or manipulation of natural enemies relies on theoretical models and a limited number of experimental studies. An important component of future research should be the effect of system productivity on higher-order predators in managed habitats. Variation in resource availability may influence the role of intraguild predation for the structure of communities and for the abundance of species.

For example, productivity in agroecosystems is a function of abiotic factors (i.e., temperature, humidity, and light) and agronomic practices (i.e., selection of plant species and crop cultivars, crop management, fertilization, and irrigation) that vary through time. This transitory, often predictable nature of agroecosystems could possibly be taken into consideration to determine suitable conditions for releasing top predators in biological control. For instance, in a system where biological control agents need to be released against herbivores, the productivity model (Fig. 1) predicts that a combination of intermediate predators should be released against herbivores because they are better competitors for the herbivore than higher-order predators.

The latter may suffer from exploitative competition and be more prone to disperse. The introduction of omnivorous predators would be a desirable strategy when herbivores are abundant, favouring co-existence of first- and second-order predators (Brodeur et al., 2002). In conservation ecology, when intraguild predation is desirable to control mesopredator populations, resources have to be kept above a minimum threshold for top predators to remain or establish as functional members of the food web. Although challenging, studying the response of intraguild predation along productivity gradients might contribute to the current effort to make biological control (Ehler, 1990; Waage, 1990) and conservation ecology more predictive sciences.

Acknowledgments

We would like to thank Joop van Lenteren and Ian Hardy for allowing this article although we both could not attend the meeting. Chris Carbone, Enrique Chagneton, Charles Godfray, Richard Pettifor, and Wilf Powell provided helpful discussion and comments on the manuscript.

References

- Abrams, P., Menge, B.A., Mittelbach, G.G., Spiller, D., Yodzis, P., 1996. The role of indirect effects in food webs. In: Polis, G.A., Winemiller, K.O. (Eds.), *Food Webs: Integration of Patterns and Dynamics*. Chapman & Hall, New York, pp. 371–395.
- Bellows, T.S., Hassell, M.P., 1999. Theories and mechanisms of natural population regulation. In: Bellows, T.S., Fisher, T.W. (Eds.), *Handbook of Biological Control*. Academic Press, San Diego, pp. 17–44.
- Bohannan, B.J.M., Lenski, R.E., 2000. The relative importance of competition and predation varies with productivity in a model community. *American Naturalist* 156, 329–340.
- Brodeur, J., Rosenheim, J.A., 2000. Intraguild interactions in aphid parasitoids. *Entomologia Experimentalis et Applicata* 97, 93–108.
- Brodeur, J., Cloutier, C., Gillespie, D., 2002. Higher-order predators in greenhouse systems. *Bull. IOBC/WPRS* 25, 33–36.
- Cisneros, J.J., Rosenheim, J.A., 1997. Ontogenetic change of prey preference in the generalist predator *Zelus renardii* and its influence on predator–prey interactions. *Ecological Entomology* 22, 399–407.
- Colfer, R.G., Rosenheim, J.A., 2001. Predation on immature parasitoids and its impact on aphid suppression. *Oecologia* 126, 292–304.
- Coll, M., Guershon, M., 2002. Omnivory in terrestrial arthropods: mixing plant and prey diets. *Annual Review of Entomology* 47, 267–297.
- Courchamp, F., Langlais, M., Sugihara, G., 1999. Cats protecting birds: modelling the mesopredator release effect. *Journal of Animal Ecology* 68, 282–292.
- Courchamp, F., Langlais, M., Sugihara, G., 2000. Rabbits killing birds: modelling the hyperpredation process. *Journal of Animal Ecology* 69, 154–164.
- Crooks, K.R., Soulé, M.E., 1999. Mesopredator release and avifaunal extinctions in fragmented systems. *Nature* 400, 563–566.

- Ehler, L.E., 1990. Introduction strategies in biological control of insects. In: Mackauer, M., Ehler, L.E., Roland, J. (Eds.), *Critical Issues in Biological Control*. Intercept, Andover, UK, pp. 111–134.
- Fenton, A., Norman, R., Fairbairn, J.P., Hudson, P.J., 2001. Evaluating the efficacy of entomopathogenic nematodes for the biological control of crop pests: a nonequilibrium approach. *American Naturalist* 158, 408–425.
- Ferguson, K.I., Stiling, P., 1996. Non-additive effects of multiple natural enemies on aphid populations. *Oecologia* 108, 375–379.
- Follett, P.A., Duan, J.J., 2000. *Nontarget Effects of Biological Control*. Kluwer Academic Publishers, The Netherlands.
- Frazer, B.D., Gilbert, N., 1976. Coccinellids and aphids: a quantitative study of the impact of adult ladybirds (Coleoptera: Coccinellidae) preying on field populations of pea aphids (Homoptera: Aphididae). *Journal of the Entomological Society of British Columbia* 73, 33–56.
- Hawkins, B.A., Mills, N.J., Jervis, M.A., Price, P.W., 1999. Is the biological control of insects a natural phenomenon? *Oikos* 86, 493–506.
- Hawkins, B.A., 2000. Species coexistence in parasitoid communities: does competition matter? In: Hochberg, M.E., Ives, A.R. (Eds.), *Parasitoid Population Biology*. Princeton University Press, Princeton, NJ, pp. 198–213.
- Henneman, M.L., Memmott, J., 2001. Infiltration of a Hawaiian community by introduced biological control agents. *Science* 293, 1314–1316.
- Hochberg, M., Lawton, J.H., 1990. Competition between kingdoms. *Trends in Ecology and Evolution* 5, 367–371.
- Höller, C., Borgemeister, C., Haardt, H., Powell, W., 1993. The relationship between primary parasitoids and hyperparasitoids of cereal aphids: an analysis of field data. *Journal of Animal Ecology* 62, 12–21.
- Holt, R.D., Lawton, J.H., 1993. Apparent competition and enemy-free space in insect host-parasitoid communities. *American Naturalist* 142, 623–645.
- Holt, R.D., Grover, J., Tilman, D., 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *Theoretical Population Biology* 11, 197–229.
- Holt, R.D., Polis, G.A., 1997. A theoretical framework for intraguild predation. *American Naturalist* 149, 745–764.
- Hoogendoorn, M., Heimpel, G.E., 2001. *Biological Control*.
- Hunter, M.D., Price, P.W., 1992. Playing chutes and ladders—heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73, 724–732.
- Karl, B.J., Best, H.A., 1982. Feral cats on Stewart Island; their foods, and their effects on kakapo. *NZ Journal of Zoology* 9, 287–294.
- Leibold, M.A., 1989. Resource edibility and the effects of predator and productivity on the outcome of trophic interactions. *American Naturalist* 134, 922–949.
- Leibold, M.A., 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *American Naturalist* 147, 784–812.
- Losey, J.E., Denno, R.F., 1998a. The escape response of pea aphids to foliar-foraging predators: factors affecting dropping behaviour. *Ecological Entomology* 23, 53–61.
- Losey, J.E., Denno, R.F., 1998b. Interspecific variation in the escape responses of aphids: effect on risk of predation from foliar-foraging and ground-foraging predators. *Oecologia* 115, 245–252.
- Losey, J.E., Denno, R.F., 1998c. Positive predator–predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology* 79, 2143–2152.
- Lucas, E., Coderre, D., Brodeur, J., 1998. Intraguild predation among aphid predators: characterisation and influence of extraguild prey density. *Ecology* 79, 1084–1092.
- May, R.M., Hassell, M.P., 1981. The dynamics of multiparasitoid–host interactions. *American Naturalist* 117, 234–261.
- McCann, K., Hastings, A.M., 1997. Re-evaluating the omnivory–stability relationship in food webs. *Proceedings of the Royal Society of London B* 264, 1249–1254.
- McCann, K., Hastings, A.M., Huxel, G.R., 1998. Weak interactions and the balance of nature. *Nature* 395, 794–798.
- Mesquita, A.L.M., Lacey, L.A., Leclant, F., 1997. Individual and combined effects of the fungus, *Paecilomyces fumosotus* and parasitoid, *Aphelinus asychis* Walker (Hym., Aphelinidae) on confined populations of Russian wheat aphid, *Diuraphis noxia* (Mordvilko)(Hom., Aphididae) under field conditions. *Journal of Applied Entomology* 121, 155–163.
- Meyhöfer, R., 2001. Intraguild predation on the aphid parasitoid *Lysiphlebus fabarum* (Marshall) (Hymenoptera: Aphididae): mortality risks and behavioral decisions made under the threats of predation. *Biological Control* 25, 239–248.
- Müller, C.B., Godfray, H.C.J., 1997. Apparent competition between two aphid species. *Journal of Animal Ecology* 66, 57–64.
- Müller, C.B., Godfray, H.C.J., 1998. The response of aphid secondary parasitoids to different patch densities of their host. *BioControl* 43, 129–139.
- Müller, C.B., Godfray, H.C.J., 1999a. Indirect interactions in aphid-parasitoid communities. *Researches on Population Ecology* 41, 93–106.
- Müller, C.B., Godfray, H.C.J., 1999b. Predators and mutualists influence the exclusion of aphid species from natural communities. *Oecologia* 119, 120–125.
- Müller, C.B., Adriaanse, I.C.T., Belshaw, R., Godfray, H.C.J., 1999. The structure of an aphid-parasitoid community. *Journal of Animal Ecology* 68, 346–370.
- Morris, R.J., Müller, C.B., Godfray, H.C.J., 2001. Apparent competition between aphid primary parasitoids via secondary parasitoids. *Journal of Animal Ecology* 70, 301–309.
- Palomares, P., Caro, T.M., 1999. Interspecific killing among mammalian carnivores. *American Naturalist* 153, 492–508.
- Palomares, P., Gaona, P., Ferreras, P., Delibes, M., 1994. Positive effects on game species of top predators by controlling smaller predator populations: an example of lynx, mongooses, and rabbits. *Conservation Biology* 9, 295–305.
- Pérez-Lachaud, G., Hardy, I.C.W., Lachaud, J.-P., 2001. Insectgladiators: competitive interactions between three species of bethylid wasps attacking the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). *Biological Control* 25, 231–238.
- Person, L., Bengtsson, J., Menge, B., Power, M.E., 1996. Productivity and consumer regulations—concepts, patterns and mechanisms. In: Polis, G.A., Winemiller, K.O. (Eds.), *Food Webs: Integration of Patterns and Dynamics*. Chapman & Hall, New York, pp. 396–434.
- Pimm, S.L., 1991. *The Balance of Nature?* University of Chicago Press, Chicago.
- Pimm, S.L., Lawton, J.H., 1978. On feeding on more than one trophic level. *Nature* 275, 542–544.
- Pimm, S.L., Lawton, J.H., Cohen, J.E., 1991. Food web patterns and their consequences. *Nature* 350, 669–674.
- Polis, G.A., 1999. Why are parts of the world green? Multiple factors control productivity and distribution of biomass. *Oikos* 86, 3–15.
- Polis, G.A., Holt, R.D., 1992. Intraguild predation: the dynamics of complex trophic interactions. *Trends in Ecology and Evolution* 7, 151–154.
- Polis, G.A., Strong, D.R., 1996. Food web complexity and community dynamics. *American Naturalist* 147, 813–846.
- Polis, G.A., Winemiller, K.O., 1996. *Food Webs: Integration of Patterns and Dynamics*. Chapman & Hall, New York.
- Polis, G.A., Myers, C.A., Holt, R.D., 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20, 297–330.
- Polis, G.A., Sears, A.L.W., Huxel, G.R., Strong, D.R., Maron, J., 2000. When is a cascade a trophic cascade? *Trends in Ecology and Evolution* 15, 473–475.

- Pope, T., Croxson, E., Pell, J.K., Godfray, H.C.J., Müller, C.B., 2002. Apparent competition between two species of aphid via the fungal pathogen *Erynia neoaphidis* and its interaction with the aphid parasitoid *Aphidius ervi*. *Ecological Entomology* 27, 196–203.
- Power, M.E., 1992. Top-down and bottom-up forces in food webs: do plants have primacy? *Ecology* 73, 733–746.
- Raymond, B., Darby, A.C., Douglas, A.E., 2000. Intraguild predators and the spatial distribution of a parasitoid. *Oecologia* 124, 367–372.
- Rogers, C.M., Caro, M.J., 1998. Song sparrows, top carnivores and nest predation: a test of the mesopredator release hypothesis. *Oecologia* 116, 227–233.
- Root, R.B., 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs* 37, 317–350.
- 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., Kaya, H.K., Ehler, L.E., Marois, J.J., Jaffee, B.A., 1995. Intraguild predation among biological-control agents: theory and evidence. *Biological Control* 5, 303–335.
- Rosenheim, J.A., Wilthoit, L.R., Armer, C.A., 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia* 96, 439–449.
- Rosenzweig, M.L., 1977. Community structure in sympatric Carnivora. *Journal of Mammalogy* 47, 602–612.
- Rott, A.S., Müller, C.B., Godfray, H.C.J., 1998. Evidence for short-term apparent competition between two aphid species. *Ecology Letters* 1, 99–103.
- Schmitz, O.J., Hamback, P.A., Beckerman, A.P., 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removal on plants. *American Naturalist* 155, 141–153.
- Schooler, S.S., Ives, A.R., Harmon, J., 1996. Hyperparasitoid aggregation in response to variation in *Aphidius ervi* host density at three spatial scales. *Ecological Entomology* 21, 249–258.
- Scott, J.K., Quimby, P.C., 2001. Evaluating Indirect Ecological Effects of Biological Control. CAB International, Wallingford, UK.
- Sih, A., Crowley, P., McPeck, M., Petranka, J., Strohmeier, K., 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* 16, 269–311.
- Sih, A., Englund, G., Wooster, D., 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution* 13, 350–355.
- Simberloff, D., Stiling, P., 1996a. Risks of species introduced for biological control. *Biological Conservation* 78, 185–192.
- Simberloff, D., Stiling, P., 1996b. How risky is biological control? *Ecology* 77, 1965–1974.
- Smith, A.P., Quin, D.G., 1996. Patterns and causes of extinction and decline in Australian conilurine rodents. *Biological Conservation* 77, 243–267.
- Soulé, M.E., Bolger, D.T., Alberts, A.C., Wright, J., Sorice, M., Hill, S., 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* 2, 75–92.
- Sunderland, K.D., Axelsen, J.A., Dromph, K., Freier, B., Heptinne, J.-L., Holst, N.H., Mols, P.J.M., Petersen, M.K., Powell, W., Ruggie, P., Triltsch, H., Winder, L., 1997. Pest control by a community of natural enemies. In: Powell, W. (Ed.), *Arthropod Natural Enemies in Arable Land III. The Individual, the Population and the Community*. Aarhus University Press, Denmark, pp. 271–326.
- Taylor, A.J., Müller, C.B., Godfray, H.C.J., 1998. Effect of aphid predators on oviposition behaviour of aphid parasitoids. *Journal of Insect Behavior* 11, 297–302.
- van Veen, F.J.F., Müller, C.B., Adriaanse, I.T.C., Godfray, H.C.J., 2002. Spatial heterogeneity in risk of secondary parasitism in a natural population of an aphid parasitoid. *Journal of Ecology* 71, 463–469.
- Waage, J., 1990. Ecological theory and the selection of biocontrol agents. In: Mackauer, M., Ehler, L.E., Roland, J. (Eds.), *Critical Issues in Biological Control*. Intercept, Andover, UK, pp. 135–157.
- Wheeler, A.G., Hayes, J.T., Stephens, J.L., 1968. Insect predators of mummified pea aphids. *Canadian Entomologist* 100, 221–222.
- Zavaleta, E.S., Hobbs, R.J., Mooney, A., 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution* 16, 454–459.