

ALTERNATIVE FOODS AS A MECHANISM TO ENHANCE A GENERALIST LADYBIRD'S PREDATION OF TARGET PREY

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INTRODUCTION

Successful biological control is the culmination of complex ecological processes (Rosenheim *et al.*, 1995). Insect ecologists and biological control practitioners have recognized a great number of the biotic and abiotic interactions that can potentially affect the success of control efforts. However, we are still limited in our understanding of when and how these interactions will be important in real, inherently complex ecosystems. We are subsequently hindered in our ability to control pest organisms by manipulating ecological processes. A better understanding of the community interactions of natural enemies and their pests will improve our predictions about how management strategies will affect pest and natural enemy processes and ultimately can help lead to better pest control.

TWO-SPECIES MODELS

Conceptual and theoretical models are important tools for gaining insights into the ecological interactions of a pest and its natural enemy. The simplest model of biological control is focused on a single resource, designated the target pest, a natural enemy that consumes the pest, and the strongest interactions between the two. This common model of biological control can be viewed conceptually with the notation of Levins and Lewontin (1985) (Fig. 1A) and is exemplified by the Nicholson-Bailey model (Nicholson and Bailey, 1935). The two interactions assumed the strongest and most important are predation and reproduction. The predator consumes the prey, thereby directly decreasing the prey's population. The prey has a positive effect on the predator population by providing a food source for maintenance and reproduction.

This two species model of biological control has become a paradigm for looking at natural enemy-pest interactions. Although not explicitly modeled, it is assumed that an increase or decrease in the herbivore will ultimately affect the host plant through cascading indirect effects as originally proposed by Hairston *et al.* (1960). Both forms of these models have historically dominated research in biological control, and have led to a number of insights, but these models, like all models, are an inherent simplification of the real system.

While there are a number of questions and systems that a two-species model can examine, recent work has demonstrated that the historical theory of trophic interactions is often insufficient for explaining predator-prey interactions. In many cases, multi-species interactions may be crucial for determining the overall pattern of success or failure in controlling a target pest. One important complication occurs when we broaden the two-species model to a three-species model, where a shared "predator" consumes the other two species (Fig. 1B). While this new three-species model is a rather simple extension from the two-species system, the result can have profound phenomenological effects.

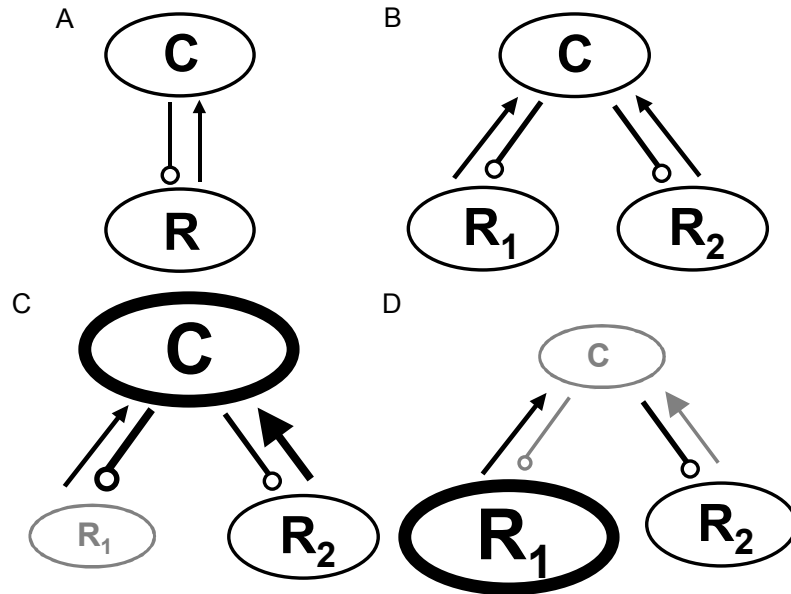


Figure 1. Principal direct interactions in two- (A) and three-species (B-D) community modules using the notation of Levins and Lewontin (1985), where an arrow represents a positive effect and line with circle identifies a negative effect. Each ellipse represents a single species: C=the consumer (e.g., generalist predator), R₁=first resource, the target pest, and R₂=the second resource. The addition of an alternative prey can diminish (C) or enhance (D) populations of the target pest as compared to the two species system (A).

THREE-SPECIES MODELS

A two-prey, one-predator system can produce a variety of patterns through direct and indirect interactions. Assuming that each of the three species is capable of having a positive, negative, or no interaction with each of the other species, there are 704 possible three species systems (3^6 minus the 25 possible no interacting or two interacting species systems). These simple interactions result in a full spectrum of potential stable and unstable dynamics for each of the participants. Including realistic processes such as self-damping or other density-dependent effects can produce further theoretical systems that also show the vast array of potential patterns that occur from simply adding a third species to a two-species community module (Schellhorn and Andow, 1999).

Native generalist predators are becoming increasingly important to conservation biological control programs and are well suited for a more complex community module with two resources sharing a consumer. In fact, it is unlikely that the only strong interactions with a generalist predator will occur with a single prey. The availability of multiple potential prey for generalist arthropod predators in an agroecosystem is more the rule than the exception, and in addition, many generalist predators are omnivorous, feeding on both plant and animal material (Coll and Guershon, 2002 and references within). The very discussion of generalist predators for biological control can be somewhat contentious. The introduction of exotic generalist predators often carries substantial risks to non-target organisms (Simberloff and Stiling, 1996). However, native generalist predators may actually be

more beneficial to conservation and augmentative biological control efforts than their better-studied specialist counterparts (DeBach, 1974; Chang and Kareiva, 1999) because they can persist and even increase their populations when the target pest is absent (Murdoch *et al.*, 1985). For generalists to persist there must be alternative food resources available. The use of multiple resources may make a generalist predator more beneficial but may also be an immediate complicating factor in understanding its effectiveness.

If we assume that we can model all resources as a single homogeneous entity, it would be sufficient to investigate generalist predators using a single-consumer, single-resource model. By increasing the number of resources in the model, we are suggesting that this assumption is insufficient for understanding the dynamics of the predator and target prey. The most obvious reason for increasing the number of resources in a model is when both potential resources strongly interact with the predator and are of different species (a generalist or polyphagous natural enemy) or even of different kingdoms (omnivorous natural enemy). In general, we may have to account for resources separately if they do not have similar fundamental dynamics, or the predator uses them differently. Different species can differ in a variety of such characteristics, but there are often subtle differences that can also lead to interesting insights by conceptualizing the interactions as a three-species system. For example, many parasitoids may use potential resources differently such that one host is best for males and another for females, or one size of host may be better for reproduction and the other for nutrient acquisition (Briggs *et al.*, 1999). Similarly, a resource may be better suited to model as two if it includes intraspecific variation that make individuals more or less susceptible to predation and parasitism due to genetic (e.g., Henter and Via, 1995) or morphological (e.g., Losey *et al.*, 1997) differences. The second resource being consumed by the shared predator may even be a predator itself, introducing higher order predator interactions such as intraguild predation (Rosenheim, 1998 and references within).

The effects of multiple resources on a single consumer have been well studied empirically and theoretically, and have been found to play a significant role in community dynamics and the natural control of insect pests (Root, 1973; Andow and Risch, 1985; Abrams, 1987; Abrams and Hiroyuki, 1996; Bonsall and Hassell, 1997; Abrams *et al.*, 1998; Chaneton and Bonsall, 2000; Eubanks and Denno, 2000; Harmon *et al.*, 2000; Coll and Guershon, 2002). Of particular relevance to biological control is a focus on the target pest to determine how the addition of a third species can affect its population. In general, the addition of a third interacting species can increase, decrease, or have no effect on the original prey compared with the single-predator, single-prey system (Abrams, 1987). Given that the addition of a third, strongly interacting species can reduce pest densities below that achieved with the two-species system, there is a tremendous opportunity to enhance pest control efforts, especially those in the realm of conservation biological control. However, because the addition of certain third species can enhance the target pest, great care must be taken in deciding management strategies that attempt to manipulate this ecological process. For successful prediction, we must better understand the types of systems best modeled as a multiple-prey community and the mechanisms their participants interact through to form ultimately influence target pests.

The addition of a second or "alternative" resource can influence the target pest through a variety of direct and indirect interactions. The two resources may interact indirectly through their shared predator. If the alternative resource has primarily a positive effect on the predator, the predator can then have a stronger negative effect on the target pest, resulting in a negative indirect effect of the alternative resource on the target pest (Fig. 1C). This phenomenon is commonly referred to as

“apparent competition” (Holt, 1977) and can occur either symmetrically or asymmetrically (Chaneaton and Bonsall, 2000). In contrast, the target pest may increase compared with the two-species system if the alternative has a net negative effect on the predator, thereby releasing the target from control of the shared predator (Fig. 1D). The target resource may also be affected if the two resources interact strongly either directly or indirectly through their shared resource, the host plant (Abrams, 1987).

The conceptual model of a three-species system can help illustrate potential pathways of indirect and direct effects and determine their qualitative outcome. However, it is still extremely difficult to make *a priori* predictions about how the potential interactions of three species will ultimately lead to quantifiable changes in the target pest. One way of improving predictive ability is to investigate the mechanisms underlying how the spatial and temporal availability of target and non-target foods affects predation of target pests. This can help develop predictive frameworks of a predator's response to food communities and the circumstances that could maximize the predator's impact on a given target prey.

An alternative resource can indirectly affect a target resource by influencing the shared predator through three potential mechanisms. These mechanisms parallel changes to a predator's numerical or functional response. First, the resource may affect the number of predators found locally by influencing predator movement. For example, dandelions can increase the local aggregation of an omnivorous ladybird in alfalfa causing the ladybird to increase its predation on aphids in patches with dandelions compared to patches without (Harmon *et al.*, 2000). Non-target resources can also change the number of consumers by influencing their reproduction. In many systems it is fairly common for ladybirds to enhance their reproduction by consuming aphids, pollen, or other resources across the landscape (Hodek and Honek, 1996). These alternative resources may thus enhance the predator's reproduction, especially early season, and subsequently increase their ability to attack later occurring pest species. Finally, the alternative resource may also affect the predator's individual behavior. Our current work (Harmon, 2003 *in prep*) is documenting how different alternative resources can also cause relatively complex and seemingly unintuitive effects on the foraging behavior of ladybirds, ultimately causing different effects on target predation depending on the characteristics of the resources available.

While multispecies communities can often produce complex phenomenological patterns, it may be possible to predict the dynamics of a given system by disentangling its numerous potential direct and indirect interactions. Just as two species models have characterized prey and natural enemies to better predict some of their interactions, it is possible to determine the characteristics of alternative prey that will ultimately enhance target predation. Characterizing potential alternative prey and the mechanisms through which they affect predator-prey systems will be an important step towards developing predictable and effective management strategies for maximizing conservation biological control with generalist predators.

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