

# Relationships of Natural Enemies and Non-Prey Foods

# Progress in Biological Control

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Volume 7

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# Relationships of Natural Enemies and Non-Prey Foods

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*Cover pictures:* The photo credits should read (clockwise from top left):

*Amara carinata* (LeConte), a common granivorous carabid in the Midwest and Great Plains of North America (photo by Jonathan Lundgren).

A mixture of seeds commonly encountered in cropland (photo by Jonathan Lundgren).

A fourth instar *Coleomegilla maculata* DeGeer, consuming maize pollen (photo by Michael Jeffords, Illinois Natural History Survey).

Adult *Coleomegilla maculata* DeGeer, foraging on the tassel of maize for pollen. This species is one of the most widespread and abundant ladybeetles in North American cropland, and is highly omnivorous on pollen, fungus, and sugar sources (Photo by Michael Jeffords, Illinois Natural History Survey).

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*This book is dedicated above all to*

*Jenna*

*My successes are brighter and failures  
are bearable because of you*

*R. N. W.*

*For the wisdom that gave me a wide berth  
to explore what I felt was important, and the  
good sense to know when to bring me back  
to reality. These are traits found only in the  
best of mentors*

# Progress in Biological Control

## Series Preface

Biological control of pests, weeds, and plant and animal diseases utilising their natural antagonists is a well-established and rapidly evolving field of science. Despite its stunning successes world-wide and a steadily growing number of applications, biological control has remained grossly underexploited. Its untapped potential, however, represents the best hope to providing lasting, environmentally sound, and socially acceptable pest management. Such techniques are urgently needed for the control of an increasing number of problem pests affecting agriculture and forestry, and to suppress invasive organisms which threaten natural habitats and global biodiversity.

Based on the positive features of biological control, such as its target specificity and the lack of negative impacts on humans, it is the prime candidate in the search for reducing dependency on chemical pesticides. Replacement of chemical control by biological control – even partially as in many IPM programs – has important positive but so far neglected socio-economic, humanitarian, environmental and ethical implications. Change from chemical to biological control substantially contributes to the conservation of natural resources, and results in a considerable reduction of environmental pollution. It eliminates human exposure to toxic pesticides, improves sustainability of production systems, and enhances biodiversity. Public demand for finding solutions based on biological control is the main driving force in the increasing utilisation of natural enemies for controlling noxious organisms.

This book series is intended to accelerate these developments through exploring the progress made within the various aspects of biological control, and via documenting these advances to the benefit of fellow scientists, students, public officials, policymakers, and the public at large. Each of the books in this series is expected to provide a comprehensive, authoritative synthesis of the topic, likely to stand the test of time.

Heikki M.T. Hokkanen, Series Editor

# Foreword

## Feeding on Non-Prey Resources by Natural Enemies

Moshe Coll

Reports on the consumption of non-prey food sources, particularly plant materials, by predators and parasitoids are common throughout the literature (reviewed recently by Naranjo and Gibson 1996, Coll 1998a, Coll and Guershon, 2002). Predators belonging to a variety of orders and families are known to feed on pollen and nectar, and adult parasitoids acquire nutrients from honeydew and floral and extrafloral nectar. A recent publication by Wäckers et al. (2005) discusses the provisioning of plant resources to natural enemies from the perspective of the plant, exploring the evolutionary possibility that plants enhance their defenses by recruiting enemies to food sources. The present volume, in contrast, presents primarily the enemies' perspective, and as such is the first comprehensive review of the nutritional importance of non-prey foods for insect predators and parasitoids.

Although the ecological significance of feeding on non-prey foods has long been underappreciated, attempts have been made to manipulate nectar and pollen availability in crop fields in order to enhance levels of biological pest control by natural enemies (van Emden, 1965; Hagen, 1986; Coll, 1998a). The importance of non-prey foods for the management of pest populations is also discussed in the book. To place our view of interactions between prey, predators and supplemental foods in a historical context, I will briefly review developments in our understanding of trophic interactions in ecological systems, from consumer-resource relationships, through interactions in linear food chains with three species, to more complex direct and indirect effects in community modules with closed loops of omnivorous interactions. Finally, I will touch upon more recent research on trophic interactions of greater complexity, and discuss the need to place omnivorous feeding habits in spatial, evolutionary and conservation biology contexts.

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# 1 From Simple Interactions in Linear Food-Chains to Omnivorous Trophic Loops

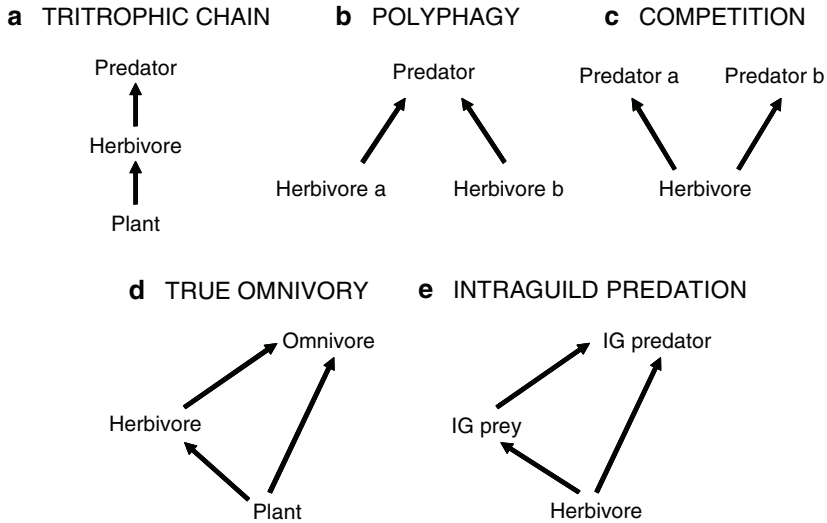
Ecologists have traditionally focused on feeding by organisms on food items at the trophic level immediately below their own. This perspective is not indicative of a belief that interactions between two trophic levels occur in isolation, but rather expresses the hope that a simplistic view of ecological systems would yield in-depth understanding of underlying processes (Begon et al. 1996a). This approach led trophic research in two general directions, one dealing with animal–plant interactions, and the other focusing on interactions between predators and their prey.

Studies of animal–plant relationships allowed for detailed investigation of the effects of plant chemistry, morphology, and structure on herbivores, and resulted in the development of numerous testable hypotheses. Although many major advances in our understanding of insect–plant interactions date back some 50 years, with notable contributions by Fraenkel (1959), Ehrlich and Raven (1964), Feeny (1975, 1976) and Rhoades (1979), ecological investigations of predator–prey and host–parasitoid interactions were initiated even earlier (Lotka, 1924; Volterra, 1926; Nicholson, 1933; Nicholson and Bailey, 1935). It should be noted that the effect of predators and parasitoids on herbivore populations was in fact appreciated more than 2,300 years ago, when natural enemies were used for biological pest control (DeBach and Rosen, 1991). It therefore seems that agricultural use of natural enemies both preceded and stimulated the ecological investigations of predator–prey interactions that gained momentum during the 20th century. Much effort over the last 50 years was therefore aimed at identifying regulators of insect populations and was focused on inter-trophic level interactions, be they herbivore–plant or predator–prey associations (Hairston et al., 1960; Hassell, 1978, 1985; Strong et al., 1984).

After the late 1970's, trophic interactions between consumers and their food sources were placed in a three-trophic level context (Fig 1a) (Campbell and Duffey, 1979; Lawton and McNeill, 1979; Price et al., 1980; Schultz, 1983). These early studies were focused on direct adverse effects of plant defenses on natural enemies, and on positive indirect influences of plants that acted to increase enemy-induced mortality by slowing herbivore development (Campbell and Duffey, 1979; Lawton and McNeill, 1979). While the traditional view, in which ecological communities are composed of distinct trophic levels, is in evidence in both early and more recent entomological studies (Pierce et al., 1912; Pearson and Dyer, 2006), later studies also focus on other trophic configurations in modules with three species. These modules include an enemy that attacks two herbivores (Fig. 1b), and a single prey which is attacked by two enemies (Fig. 1c).

More recently, ecologists have addressed interactions of greater complexity in three-species community modules (e.g., Polis, 1991; Polis and Holt, 1992; Coll and Guershon, 2002; Finke and Denno, 2004). The widely accepted view of communities as consisting of species occupying three functionally discrete trophic levels, as proposed by Hairston et al. (1960), has been replaced by a recognition of the importance of modules containing omnivorous species, defined as consumers that feed at more



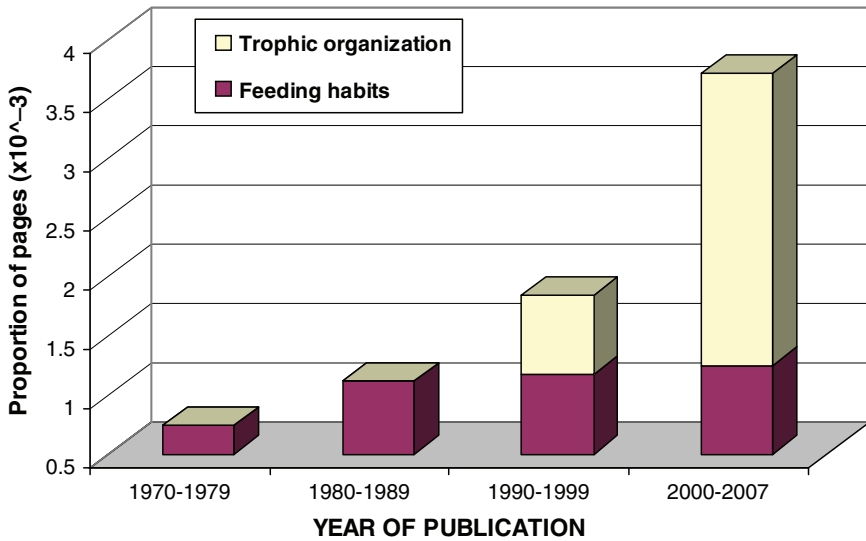


**Fig. 1** Diagrammatic representation of possible direct trophic relations in community modules composed of three species. Feeding also on the plant by the predator in module (a) will result in true omnivory (d); two prey species with a shared predator (b) may exhibit apparent competition; and a predator feeding on the second predator in module (c) will lead to intraguild predation (e) of the intraguild (IG) prey by the IG predator. Both true omnivory (d) and intraguild predation (e) are cases of trophic omnivory, whereby the omnivore and IG predator feed at more than one trophic level

than one trophic level (Pimm and Strong 1978). These modules, which act to blur trophic organization, include closed loops wherein one species, be it the herbivore in true omnivory (Fig. 1d) or the intraguild (IG) prey in the case of IG predation (Fig. 1e), is not only consumed by top predators (the omnivore and IG predator), but also competes with them for shared food sources (plant and herbivore).

Indeed, examination of ecology textbooks<sup>1</sup> reveals an exponential increase in the attention devoted to omnivory over the last 40 years (Fig. 2); yet, data show that until the early 1990's, the term omnivory appeared in these books only to describe the nature of animal feeding habits, much like herbivory and carnivory. This use of the term omnivory dates back to ancient Greece. Aristotle, who is regarded as the founder of the biological sciences, recognized that terrestrial animals differ in their diets: they can be carnivorous, graminivorous, omnivorous, or "special" (e.g., nectivorous)

<sup>1</sup>The indexes of 27 authored, general ecology and insect ecology textbooks were examined for the number of pages that include the words 'omnivory', 'omnivore' or 'omnivorous' in the volume. The number of pages with the terms was divided by the total number of text pages in the volume to obtain the "attention level". Then, the context in which the terms appear in the text was classified as "feeding habit" (much like herbivory and carnivory) or "trophic organization".



**Fig. 2** Change over time in the attention devoted to omnivory in ecological textbooks. Shown is the proportion of pages in authored general ecology ( $n = 22$ ) and insect ecology ( $n = 5$ ) textbooks<sup>2</sup> in which the terms ‘omnivory’, ‘omnivore’ or ‘omnivorous’ appear, as indicated by the books’ subject indexes. Each mention of the terms in the text was then classified as based on ‘feeding habits’ or ‘trophic organization’ according to context

(outlined by Allee et al., 1949: 15). Discussion of trophic omnivory and its significance for community structure and function has appeared in textbooks only very recently, with a four-fold increase in attention between the 1990s and 2000s (Fig. 2). A similar situation came to light when the glossary definitions of ‘omnivory’ or ‘omnivore’ found in these books were compared ( $n = 14$ ). Six of the glossaries did not define ‘omnivory’ at all; the trophic definition of omnivory appeared only after 1990; and only one glossary (Ricklefs, 1990) lists both definitions. I argue that the changes appearing in the definitions of these terms act to confuse trophic and true omnivory, thus obscuring peculiarities of the latter. A case in point is the definition used by Begon et al. (2006b) of omnivory as ‘feeding on prey from more than one trophic level’ that excludes true omnivory altogether.

The present volume deals primarily with true omnivory; it is a timely compilation of our understanding of the nutritional, ecological, and agricultural significance of feeding on non-prey foods, be they fungi, or plant- or herbivore-produced materials.

<sup>2</sup>Begon et al. (1986, 1990, 1996b, 2006); Chapin et al. (2002); Chapman and Reiss (1992); Colinvaux (1993); Dodson et al. (1998); Krebs (1972, 1978, 1994, 2001); McIntosh (1985); McNaughton and Wolf (1979); Odum (1971, 1983); Price (1975, 1984, 1997); Ricklefs (1973, 1990, 1997); Ricklefs and Miller (2000); Schowalter (2006); Smith (1974); Speight et al. (1999); and Townsend et al. (2003).

This comprehensive contribution, together with other publications which have appeared over the last 12 years (Alomar and Wiedenmann, 1996; Jervis and Kidd, 1996; Schaefer, 1997; Coll, 1998b; Coll and Guershon, 2002; Wäckers et al., 2005), encompasses many aspects of plant-feeding by natural enemies which need not be repeated in this foreword. I will instead focus in the remainder of this chapter on several little-studied implications of true omnivory.

## **2 Some Ecological Implications of True Omnivory**

The dramatic change in our view of the structure of animal communities, from discrete to more diffused trophic organization, presents ecologists with new research challenges. I briefly discuss some of these challenges in this section.

### ***2.1 Synergistic Nutritional Effects on True Omnivores***

Omnivorous predators are assumed to switch between prey and plant feeding (Cohen, 1996; Naranjo and Gibson, 1996; Coll, 1998b; Agrawal et al., 1999; Coll and Guershon, 2002), but little is known about the nutritional relations between these vastly different food sources. If prey and plant-based foods are in principle nutritionally equivalent, more herbivores should be consumed by omnivores when plant quality decreases (Agrawal et al., 1999; Eubanks and Denno, 2000, Janssen et al., 2003). Plant materials, on the other hand, may provide some essential nutrients that facilitate prey consumption. It has recently been reported that consumption of plant-derived water facilitates prey feeding in *Dicyphus hesperus* (Gillespie and McGregor, 2000; Sinia et al., 2004). Plant tissue may also provide nutrients that are not available in prey; in this case, omnivores can be expected to switch between plant- and prey-feeding to supplement their dietary needs. Exploring the nutritional interactions between plant and prey foods would help us predict short and long term effects of omnivores on herbivore populations.

### ***2.2 Foraging Behavior by True Omnivores***

Foraging strategy often affects the diet of consumers; sit-and-wait predators, for example, may be able to consume mobile but not sessile prey (see discussion in Rosenheim and Corbett (2003)). If this is the case, then we may expect true omnivores to be less mobile than pure carnivores, as they may feed on plants when plant and prey foods are nutritionally equivalent. This proposition has not been tested for true omnivores, although resolving the issue may help both to predict the ability of omnivores to suppress various prey species that differ in their mobility, and to

inform us about the susceptibility of omnivores to their own predators: it has been proposed, for example, that true omnivores are more likely to serve as IG predators than as IG prey (see discussion below).

Another important, yet little explored topic is the effect of prey and plant foods on patch dynamics of true omnivores. It is often assumed that omnivores, because they may sustain themselves on plant materials, are less likely than pure carnivores to leave the habitat when prey becomes scarce. Yet few studies have actually addressed this issue in depth (but see Eubanks and Denno, 1999). Van Laerhoven et al. (2006) showed that both plant and prey foods influence the length of time individual bugs remain on a given host plant. Investigating specific contributions of prey and plant resources to omnivore behavior in habitat patches is particularly challenging because plant resources, unlike prey, are not usually depleted by the omnivore, and the plant defines the prey's habitat. Foraging omnivores may therefore encounter both food types simultaneously; finding one type is likely to be dependant on finding the other. This dependence is likely to be asymmetrical: although finding the plant may not always result in encountering prey, the reverse is more likely to be true. Finally, nutritional constraints are often assumed to be the primary, if not the only, cause for food mixing by omnivores. Singer and Bernays (2003) pointed out that other considerations, such as toxin dilution and predator avoidance, may also lead to omnivorous feeding habits.

### ***2.3 Competition and Cannibalism by True Omnivores***

In food webs with omnivorous trophic loops, the omnivore also competes with its prey for shared food sources. It has been predicted that these competitive interactions will destabilize such three-species modules and make omnivory rare in nature (Pimm and Lawton, 1978). Theoretical studies indicate that IGP systems will persist only if the IG prey is superior to the IG predator as an exploiter of the herbivore (see discussion in Rosenheim and Harmon, 2006 and Janssen et al., 2006). This prediction is also plausible for three-species modules which include true omnivores. With a few exceptions, the nature of competitive interactions between true omnivores and their prey nonetheless remains in the realm of theory.

Contrary to predictions for IGP systems, Coll and Izraylevich (1997) showed that the true omnivorous bug *Orius insidiosus* displaces its thrips prey from preferred feeding sites on plants. The study, however, did not compare host plant utilization by the omnivore and by its prey. Instead, a heuristic mathematical model showed that a decrease in plant palatability for the omnivore tends to stabilize the system (Coll and Izraylevich, 1997). Taken together, these results support predictions formulated for IGP systems and suggest that three-species modules with true omnivores may persist on well-defended plants that adversely affect the omnivore but not the herbivore. This may result in a higher prevalence of true omnivores in systems with more monophagous than polyphagous herbivore prey, and in natural rather than managed ecosystems. These predictions await testing.

True omnivory may also reduce cannibalism because of the availability of plant-based foods (Coll and Guershon 2002). Recent studies indicate that the presence of plant materials, much like prey, does indeed reduce the intensity of cannibalism by an omnivorous bug (Leon-Beck and Coll, 2007), and that plant characteristics have an important effect on cannibalism in another true omnivore (Laycock et al., 2006). The presence of pollen also reduced cannibalism in field populations of a true omnivorous coccinellid (Cottrell and Yeargan, 1998). Yet, true omnivores may exhibit intraspecific competition for plant resources. Groenteman et al. (2006) showed, for example, that *Orius albidipennis* females guard preferred oviposition sites on cotton leaves against conspecific females, and that this behavior is more pronounced on nitrogen-rich than on nitrogen-poor plants. Likewise, proportionately fewer eggs were deposited by *O. albidipennis* at preferred sites in the presence of two intraguild predator species than in their absence (Groenteman, 2004).

## 2.4 True Omnivory and Population Dynamics

Much progress has been made in recent years in our understanding of dynamic properties of omnivore populations. Most of this progress, however, involves omnivores that feed on herbivorous and carnivorous prey (discussed recently by Janssen et al., 2006; Rosenheim and Harmon, 2006; Denno and Finke, 2006). Relatively little is known about the population dynamics of true omnivores (Coll and Izraylevich, 1997; Lalonde et al., 1999; Gillespie and Roitberg, 2006). Three unique features of these modules call for more theoretical explorations. First, works to date have treated plant-based foods as non-depletable resources. This is hardly the case in natural systems, where availability of these foods often varies over time and space and therefore is likely to change the intensity of omnivore–prey interactions. The ways in which these changes in resource availability affect the dynamics of the system remain to be studied.

The second unique feature of these systems involves the nature of the competitive interactions between true omnivores and their prey, whether characterized by exploitation (scramble) or by interference (contest) competition. Exploitation competition may occur when availability of resources such as nectar is inversely related to omnivore density, whereas interference competition has been reported when the omnivore displaces its prey from preferred feeding sites (Coll and Izraylevich, 1997). These two types of competition may have different effects on the behavior of community modules with true omnivory.

The third important feature is the differential suitability of various foods for the omnivore. The multifaceted difference in nutritional properties of plant and prey food sources often leads to differential contributions to the survival, development and fecundity of the omnivore (Coll, 1998b). For this reason, modeling of age-structured populations is expected to yield different predictions because of the diverse effects diet mixing has on various fitness traits of the omnivore.

## 2.5 *True Omnivory and Intraguild Predation*

It has been hypothesized that true omnivores will sustain themselves on plant resources when prey density is low, rather than being forced to leave the habitat or starve, as is the case for pure carnivores (Coll, 1998b; Coll and Guershon, 2002; Sabelis and van Rijn, 2006). Therefore, plant-feeding omnivores are expected to remain in the habitat and prevent subsequent rapid build-ups of herbivore populations (Coll, 1998b; Eubanks and Denno, 2000; van Rijn et al., 2002). This unique characteristic of omnivorous natural enemies is particularly desirable for biological control early in the growing season, when true omnivores can colonize fields before pests become abundant, and for regulation of pest populations exhibiting transient declines during the season. Yet when pests are scarce and true omnivores are expected to express their special advantage, the intensity of intraguild predation (IGP) also increases (Polis et al., 1989; Gillespie and Quiring, 1992; Lucas et al., 1998; Rosenheim, 2001). It is important to realize, however, that the two phenomena – true omnivory and IGP – are in many cases expressions of the single underlying fact that predators have broad diets. Many, though not all, predators whose diets are wide enough to include both prey and plant-based foods, will consume both herbivorous and carnivorous prey (Arim and Marquet, 2004). Thus, many omnivores are also IG predators, and communities that are rich in true omnivores will contain many IG predators as well. It therefore may be inappropriate to treat true omnivory and IGP as separate ecological phenomena, as has been done in the past.

In systems that include true omnivores engaged in IGP, supplementation by pollen and other plant foods is expected to have two counteracting short term effects on prey populations. First, pollen-feeding by the two predators will release prey populations from predation because factors such as gut fullness are important determinants of predator attack rate (Sabelis, 1990). This would result in greater abundance of prey in the presence of pollen. In contrast, supplementation by pollen will lessen the disruptive effect of IGP on prey suppression, i.e., it will reduce predation on the IG prey by the IG predator, which should lead to lower prey densities. A recent study on a system containing two true omnivores that are engaged in IGP confirmed these predictions by showing that both the IG prey and IG predator consumed significantly more prey in the absence of pollen than in its presence. Likewise, fewer IG prey were consumed by the IG predator in the presence of pollen than in its absence. Thus, results show that trophic interactions are weakened in the short term by supplementation with plant-based foods.

It is much harder to predict how such short term effects influence the behavior of these systems in the long run. The various ways in which plant quality affects IGP by true omnivores have been explored recently by Gillespie and Roitberg (2006). They conclude that understanding the influence of plants on IGP is important because they are likely to mediate IGP by true omnivores. Assessment of IGP occurrence in 113 food webs suggests that true omnivorous species are less likely than expected to be IG prey in nature, and more likely than expected to be IG predators (Arim and Marquet, 2004). These results suggest that the ability of IG predators to feed on non-prey foods may relax predation on and competition with

IG prey, thus allowing such IGP systems to persist. Also, true omnivorous IG prey are likely to be excluded by IG predators and thus be under-represented in food webs, if true omnivores are inferior predators relative to pure carnivores, as suggested by Coll and Guershon (2002). This issue is being explored recently also in theoretically and empirically studies of the effect of food supplements on the dynamics of community modules with IGP (Daugherty et al., 2007).

## ***2.6 Spatial Dynamics of True Omnivore Populations***

The consumption of prey and plant-derived foods by true omnivores may be separated not only in time (e.g., life-history omnivory; Polis and Strong, 1996), but also in space. If true omnivores and their prey respond differently to spatial variation in the availability of plant and prey food, the intensity of trophic interactions is expected to vary spatially, which may allow the system to persist over a larger spatial scale. This may be the case for the omnivorous bug *Anthocoris nemoralis*, which moves between tree species in Mediterranean woods to feed on pollen and different psylla species (Shaltiel and Coll, 2004). Similar disjunct distributions of omnivores and their foods can occur on a smaller scale. Recently showed that the spatial dynamics generated when true omnivores and their prey track food sources differently on the plant, and possibly when prey alter their distribution to escape predation, lead to site-specific configurations of interacting populations. Specifically, omnivorous bugs and mites congregated on pollen-bearing flowers, whereas their thrips prey colonized the fruits. The intensity of resulting trophic interactions was weakened by the heterogeneous distribution of plant and prey foods. Similar ideas were put forth by Tilman (1982), who argued that competing species may persist in a region if the supplies of different resources vary in space. Asynchronous spatial dynamics in the availability of plant and prey foods thus may enable true omnivores and their prey to coexist in heterogeneous areas. Further empirical and theoretical exploration of spatial aspects of omnivory is likely to enhance our understanding of the stability properties of these systems.

## ***2.7 Evolutionary Transition to True Omnivory***

Little is known about the adaptive advantages and disadvantages of omnivory and about constraints to the evolution of true omnivory (but see Diehl (2003) and Roitberg et al. (2005)). Studies of morphological, physiological, and behavioral traits associated with true omnivory are scant (see discussions by Coll and Guershon, 2002 and Eubanks et al., 2003), and the evolutionary path to omnivory has been the subject of extensive debate. This debate is well documented for the Heteroptera, an order encompassing diverse feeding habits and many true omnivorous species (Cobben, 1978; Sweet, 1979; Schuh, 1986; Wheeler, 2001; Eubanks

et al., 2003). Investigating the evolutionary consequences of the ability to feed on both plants and prey provides a unique opportunity to gain valuable insight into the speciation processes driven by food diversification.

## ***2.8 True Omnivory, Conservation Biology and Global Climate Changes***

Our new view of the structure and function of ecological communities as possessing diffused trophic organization, should also change our decisions concerning both conservation and the impacts of global climate changes on ecological systems. I bring three examples for such considerations. The first, which deals with invasion biology, suggests that true omnivores may pose the highest risk of invading new areas (Berkvens et al., 2008). This can be expected if polyphagous consumers are more successful invaders than specialist ones (Vázquez, 2005). If this prediction holds true, our efforts in curbing biological invasions should be directed accordingly. The second example addresses the difficulty of identifying species that warrant protection in communities with complex food webs (i.e., with many omnivores). The concept of ‘keystone interaction’ may be useful in such cases, as it refers to those pair-wise interactions whose disturbance may alter the function of the whole community (Eubanks and Styrsky, 2006). The last example applies to the implications of true omnivory for predicting the impact of global changes on ecological systems. Until recently, the effect of atmosphere enrichment with CO<sub>2</sub> has been assessed mostly for plants and, to a lesser degree, for herbivorous arthropods. Much less is known about the flow-on effects of elevated CO<sub>2</sub> on the performance of natural enemies, and nothing was known until recently about its direct and indirect effects on true omnivores (Coll and Hughes, 2008). A recent study showed that elevated CO<sub>2</sub> may (1) benefit the omnivore indirectly by slowing prey development and thus increasing its vulnerability to predation, but (2) hamper omnivore development because of reduced nitrogen content of plant foliage on which it feeds (Coll and Hughes, 2008). These examples illustrate some of the dramatic ways in which our ability to make predictions and take effective action may be altered by considering the omnivorous feeding habits of consumers in ecological communities.

## **3 Closing Remarks**

This single-authored book provides a comprehensive review of the basic ecological and applied significance of feeding by predators and parasitoids on non-prey foods, a topic that was largely ignored until recently. The author brings to the volume valuable experience in the field. It is my hope that the present volume as a whole, and my thoughts in the second part of the foreword, will encourage further exploration



of the poorly understood implications of omnivorous feeding habits for the function of ecological communities and the management of pest populations.

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# Preface

A growing proportion of the research devoted to top-down regulation of herbivore communities has been devoted to the complexity that is present in nearly all food webs. Much attention has been given to intraguild interactions among predators and parasitoids, and the importance of omnivory by these same organisms to both intra- and interguild interactions is too often ignored or trivialized. The current state of knowledge regarding the use of non-prey foods by natural enemies is diffuse. An extensive body of literature exists for glucophagy by parasitoids, and granivory by omnivorous epigeal predators (ants and carabids) is also well developed although less well synthesized. Pollinivory and mycophagy, although occasionally discussed within the context of natural enemy nutritional ecology, is relatively poorly understood. This book represents the first attempt to congeal these disparate sources of the literature to illustrate just how pervasive omnivory is within higher trophic levels, and to highlight the evolutionary interactions that have helped to shape both entomophagous arthropods and the non-prey foods themselves.

The book arose from a series of rejections. Initially, an extensive (perhaps too extensive) review of pollinivory by natural enemies was prepared (what essentially became Section II), and I tried shopping it around to several journals. Both my youth and the page limitations of the journals contributed to several rejections. I contacted Heikki Hokannen (then editor-in-chief of *BioControl*), who again explained that the article was simply too long. But rather than leaving it there, he presented that if I wanted to expand the idea, he would consider it as a title for the *Progress in Biological Control* series that Springer had entrusted him with editing. After some negotiations, I committed to a 250 page expansion of the review article, but in completing the first 250 pages, I realized that the book was only half finished. Although a bit later than hoped, the current volume is what eventually materialized, thanks to the patience of all those involved.

The goal of the book was to summarize much of the literature pertaining to the fascinating relationships that natural enemies have with non-prey foods. In initial preparations, it became very clear that to include omnivory on vegetative plant tissues would become grossly unmanageable, and so I decided to focus on fungi and microorganisms, sugar sources, pollen, and seeds as the major food categories addressed by the book. At every opportunity, I have attempted to give credit to my forebears that have provided synthesis to particular topics dealt with in this book as

I attempted to provide broader synthesis of the topic of omnivory and the influences of non-prey foods on the dynamics and ecological functions of higher trophic levels. It is my hope that this book will inspire additional research on this topic, and will help to elevate the level of attention that is given to omnivory by naturalists and applied scientists alike.

Brookings, South Dakota

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For their extremely helpful and thought-provoking comments on drafts of selected portions of this manuscript, my thanks go out to Mickey Eubanks, George Heimpel, Heikki Hokkanen, Pavel Saska, Paul van Rijn, Felix Wäckers, Don Weber, Paula Westerman, and Livy Williams. Moshe Coll provides a particularly thought-inspiring foreword on the current state of knowledge and possible futures looming for omnivory and biological control.

The species names discussed in the book were extracted from literature dating back 130 years, and many have been revised. Many thanks to the following systematists and databases that were used to provide the most update nomenclature for the discussed taxa.

*Sternorrhyncha*: Colin Favret (SEL, Beltsville, MD) and the Scalenet website (<http://www.sel.barc.usda.gov/scalenet/query.htm>);

*Plants*: Gary Larson (SD State University) and the Plants Database maintained by the USDA (<http://plants.usda.gov/>);

*Parasitoid Hymenoptera*: Jim Whitfield (University of Illinois, Urbana, IL) and the Nomina Insecta Nearctica database: (<http://www.nearctica.com/nomina/main.htm>);

*Phytoseiidae*: Hans Klompen (Ohio State University) and De Moraes, G. J., McMurtry, J. A., Denmark, H. A. Campos, C. B. 2004. A revised catalogue of the mite family Phytoseiidae. *Zootaxa*, 434, 1–494;

*Diptera*: Evenhuis, N. L., Pape, T., Pont, A. C. & Thompson, F. C. (eds.). 2008. Biosystematic Database of World Diptera. (<http://www.diptera.org/biosys.htm>). Accessed on 8 June 2008);



*Formicidae*: Bolton, B., Alpert, G., Ward, P. S., and Naskrecki, P. 2007. Bolton's Catalogue of Ants of the World 1758–2005. Harvard University Press; CD format.

*Heteroptera*: Dr. Henry Thomas (SEL, USDA-ARS, Beltsville, MD).

*Carabidae*: Kip Will (University of California, Berkeley, CA) and Lorenz, W. 2005. Systematic List of Extant Ground Beetles of the World, 2nd Edition. Published by the author, Tutzing, Germany. 530 pp.

*Neuroptera*: Oswald, J. D. (chief editor). Lacewing Digital Library. Lacewing Digital Library module. <http://lacewing.tamu.edu/>. Accessed on 29 July 2008.

Other species were checked to the best of my ability using various on-line resources.

The USDA-ARS allowed me to devote time and federal resources to researching this book (mention of any proprietary products does not constitute endorsement on behalf of the USDA). Staffs at the libraries of the University of Illinois, South Dakota State University, and the National Agriculture Library provided considerable help to locate rare or old resources. My thanks also goes out to Springer, especially Zuzana Bernhardt, Ilse Hensen, Ineke Ravesloot, and their colleagues who helped with the logistics that advanced this project to its fruition and for their patience when the project's completion dragged on longer than anyone had hoped or anticipated. Finally, this book builds upon the ideas and research put forward by my colleagues (living and dead); I hope that this volume does service unto them and inspires additional research that widens our perspective on how predators and parasitoids function within complex food webs.

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