OMNIVORY IN TERRESTRIAL ARTHROPODS:  
Mixing Plant and Prey Diets

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Abstract  Many terrestrial communities include omnivorous arthropods that feed 
on both prey and plant resources. In this review we first discuss some unique morpholog-
ical, physiological, and behavioral traits that enable omnivores to exploit such dissimi-
lar foods, and we explore possible evolutionary pathways to omnivory. We then examine 
possible benefits and costs of omnivory, describe the relationships between omnivory 
and other high-order complex trophic interactions, and consider the stability level of 
communities with closed-loop omnivory. Finally, we explore some of the implications 
of omnivory for crop damage and for biological, chemical, and cultural control prac-
tices. We conclude that the growing realization of the ubiquity of omnivory in nature 
may require a change in our view of the structure and function of ecological systems.

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SCOPE AND TERMINOLOGY

Naturalists have long been fascinated by the way animals seek and consume their food. What can be more apparent in the field than a caterpillar feeding on a young leaf or a lady beetle feasting on aggregated aphids? In their attempt to explore the order of nature, early ecologists adopted the naturalist’s perspective and categorized organisms according to their major source of energy (i.e., producers, primary consumers, secondary consumers, and so on). Implicit in this approach is that consumers derive energy and nutrients from organisms that occupy the trophic level immediately below their own. Thus, much effort has been devoted, maybe justly so, to the study of interactions between species occupying adjacent trophic levels, such as herbivores and host plants, predators and prey, and parasites and hosts (96). Sporadically, however, observations on other more complex interactions appeared in the literature. For example, blood-sucking was reported in herbivores such as tingids, coreids, cicadellids, moths, and even a weevil species (95), and pollen-feeding was recorded in predatory anthocorids, reduviids, coccinellids, phytoseids, and even spiders (for references see Table 1, see the Supplemental Material link at www.annualreviews.org). In the past few decades, it has become clear that many insects, mites, and other terrestrial arthropods are in fact omnivores, in that they obtain nutrients from both plant and prey resources. In the literature we reviewed, more than 40 insect families that belong to 12 orders include at least one omnivorous species (Table 1, www.annualreviews.org). Omnivory is exhibited also by mite, spider, and millipede species (Table 1, www.annualreviews.org).

Feeding on prey and plant resources may be separated in time, occurring at different life stages (i.e., life history omnivores). This is quite common in arthropods; for example, some adult lacewings feed on pollen, whereas their larvae are carnivorous (21). Likewise, feeding on plants and prey may be separated spatially, as in adult parasitoids that feed on nectar in unmanaged habitats and on their hosts that are abundant in cropland. Finally, omnivory can also be incidental if small prey items are ingested by an herbivore together with plant material; for example, late-instar cabbage loopers consume whitely eggs and young nymphs while feeding on collard leaves (92). Larvae of the geometrid *Prochoerodes truxaliata* ingest midge larvae present in the terminal galls on which it feeds (149). The unique traits that allow omnivores to feed on such diverse food sources and their role in community structure and function warrant special attention. Also, these insects should be studied as they may represent an evolutionary link between herbivores and carnivores.

To follow the linguistic definition, omnivores are consumers that feed on both animals and plants, or animals and fungi (28, 93). It should be stressed from the onset that an insect is considered an omnivore only if it feeds on both plants and prey in nature. Numerous terms, such as zoophytophagous, phytozoophagous, intraguild predator, prey-feeding omnivore, plant-feeding omnivore, and facultative carnivore, have been used in the literature interchangeably (39, 153, 169; and chapters within 8). Omnivores may be classified according to their diet or by their role in ecological food webs. The diet-based classification is rather straightforward:
Omnivores are placed in a category of their own, much like herbivores, carnivores, and detritivores. Omnivory is divided into opportunistic, obligatory, and facultative types based on the relative importance of plant and prey materials to the insect’s performance. Thus, opportunistic omnivores, being either carnivorous or herbivorous, can be placed near the extremes of the continuum between phytozoophagy (i.e., prey-taking herbivores) and zoophytophagy (plant-feeding carnivores).

To classify omnivores according to their ecological role in food webs, we need to refer to Pimm & Lawton’s (135) definition of an omnivore as a consumer that feeds on resources at more than one trophic level. This phenomenon is commonly termed “trophic omnivory,” to distinguish it from “true omnivory.” True omnivory therefore is a particular case of trophic omnivory in which the consumer feeds on both plants and prey (Figure 1c, d). Another example of trophic omnivory is intraguild predation, in which a predator consumes other predators with which it shares common herbivore prey (140, 141; Figure 1a).

From an ecological perspective, we recognize two types of true omnivores, intra- and interguild omnivores (Figure 1c, d). In the former type, the omnivore and its prey feed on the same host plant, whereas in the latter type they do not. Systems that include true omnivores differ in several important ways from those containing trophic omnivores. Because plant and prey diets differ greatly in their chemical composition, anatomy, and nutritional value, mixing them in the diet requires specific physiological and morphological adaptations (e.g., digestive enzymes, mouthparts). Likewise, plants and prey usually deploy different defense strategies that omnivores need to overcome (e.g., chemical defense versus escape behavior), and variations in food quality may be important in plants but less so in prey items. Therefore, plant and prey resources may complement each other nutritionally, yet they may require temporal separation of feeding bouts. It is unlikely that the quantity of plant resources plays a major role in food resource utilization because of the large difference in size between omnivorous insects and the plants on which they feed. Thus, the high availability of plant material in a habitat could allow alternate plant and prey feeding, perhaps irrespective of prey density. Also, in most cases, plants, in contrast with prey, are not removed after a feeding event. Therefore, the probability of locating a plant does not change with time. Finally, the search for and location of plant and prey resources are not mutually independent because plants define the phytophagous prey’s habitat, and searching for prey may also result in the location of suitable plant sources.

The important differences between true and trophic omnivory warrant separate treatment. Aspects of trophic omnivory have been discussed extensively (e.g., 50, 51, 134, 135, 137–142, 149, 181). Data show that trophic omnivory is extremely common in nature, occurring in various aquatic and terrestrial systems, and in temperate, subtropical, and tropical climates (87). In fact, in some systems nearly all consumers may be omnivores (141). Nonetheless, most evidence for gained adaptive benefits of omnivory is from plant-feeding omnivorous species (141). It is therefore important to distinguish between these two types of omnivory and treat them separately.
In this review we explore properties that enable insects to exploit both plant and prey resources, discuss the ecological attributes of systems that include omnivorous insects, and review the implications of this phenomenon for pest control. Owing to the broad interdisciplinary nature of omnivory and space limitations, our treatment will be extensive, rather than intensive, as we use selective data as examples. We primarily address the condition in which plant and prey food sources are actively sought and consumed during the same life stage of the omnivore. We consider food sources that include living cells such as blood, pollen, sperm,
spermatophores, ova, and feeding that involves injury to living tissues. Therefore, we do not cover herbivores that feed on animal secretions such as sweat, tears, honeydew, urine, droppings, pellets, and dung, although Jervis & Kidd (93) treat honeydew feeding as indirect feeding on plants. We also do not address the consumption of unicellular organisms. We do, however, treat nectar feeding as herbivory because its consumption is so ubiquitous in nature, and unlike sweat, tears, and honeydew, nectar production can benefit the plant only if it is consumed by other organisms. Thus, butterflies such as *Dryas iulia* (Heliconiidae) that as adults feed on both nectar and caiman and turtle tears (95) are considered herbivores, whereas adult parasitoids that feed on both nectar and their hosts (by host-feeding) are considered omnivores. Blood is included as an animal food source in this review, but we do not specifically address the unique adaptations associated with its exploitation. Finally, we do not treat cannibalism separately. This behavior, exhibited by many herbivorous insects and thus making them omnivores, has been reviewed and discussed extensively in recent years (55, 155).

**CHARACTERISTIC TRAITS OF OMNIVORES**

Feeding on food sources as diverse as plants and prey requires specialization of mouthparts, digestive tract, enzyme complexes, and biochemical pathways. In this section, we summarize information, although scant at times, on such morphological and physiological traits, as well as behavioral and phylogenetic characteristics of omnivores.

**Morphological Traits**

Insect mouthparts are commonly studied anatomical structures, often serving as the subject of research on the relationship between structure and function. Yet the majority of the studies that examine the relationship between mouthpart morphology and specific feeding habits focus on either carnivores or herbivores, whereas only a few involve omnivores (see 101 and references therein).

In a comparative study of 22 dermapteran species, the incisive area occupies two thirds of the total mandibular length in carnivorous species but was restricted to half the mandibular length in phytophagous and omnivorous ones (175). Studies of coccinellid species have reported that denticulate apical teeth and setae characterize the mandibles of phytophagous species; those of mycophagous species possessed secondary teeth on the ventral apical tooth, used for spore collection. Carnivorous species had mandibles with a unidentate or bifid apex (123, 152). A rake-like structure on the mandibles, which is thought to facilitate pollen and fungal spore collection, was found in *Tytthaspis sedecimpunctata* and *Coccinella nigrovittata* (= *T. trilineata*) (146). Both species are true omnivores, known to feed on pollen, fungal spores, mites, aphids, and thrips (147). The feeding habits and mouthpart morphology of Heteroptera have been studied extensively. In general, mandibular styles of zoophagous heteropterans are armed with back-curving teeth, which enable them to grasp struggling prey (31, 36). In contrast, those of phytophagous
heteropterans may possess teeth that curve forward toward the plant or may have no teeth at all (35, 36). The stylets of omnivorous *Deraeocoris* and *Lygus* species lack notable teeth (36). Further, some heteropterans form a stylet sheath during feeding, generally believed to act as a sealing device improving the transfer of fluids to the mouth and stabilizing mouthparts while feeding. The formation of the stylet sheath is considered to characterize herbivorous bugs (31). However, some omnivores and predators also produce the sheath (35, 36).

Based on feeding habits and related physiological and morphological traits, McMurtry & Croft (118) classified phytoseiid mites into spider-mite specialists, generalist predators, and specialized pollen-feeding omnivores. The mouthparts of some omnivorous phytoseiids are uniquely shaped, with relatively small chelicerae that possess a convex inner surface and minute denticles at the edge of the fixed digit. This shape is accompanied by a wide deutosternal groove. Both features are believed to constitute adaptations for feeding on pollen (63, 64, 118, 174).

The morphology of the digestive tract and its relation to feeding habits have been studied to a lesser extent than the mouthparts. Comparative studies of the functional morphology of arthropods’ digestive apparatus include coleopterans (66, 114), orthopterans (65, 124), soil-dwelling insects (73), and a number of mite orders (6, 52). Generally, carnivorous arthropods have a more chitinized and toothed armature in the foregut and a simpler, shorter, and less differentiated midgut in comparison with herbivorous species. One outstanding example is the inference of omnivory and even predominant carnivory for *Gryllotalpa africana*, a member of the Gryllotalpidae, a family known to be mainly herbivorous, based on gut morphology and its content (124).

**Digestive Enzymatic Traits**

Digestive systems of herbivores and carnivores are expected to differ from each other in accordance with the pronounced differences in the chemical composition of the food they consume, particularly the inverted protein-carbohydrate ratio of plant versus animal tissue (159, 180). Early studies reported the absence of proteases and amylases from the saliva of sap feeders (125). Accordingly, proteases and phospholipases have been found in the salivary glands of all insect predators tested, but not in those of some phytophagous bugs such as *Poecilocapsus lineatus* (Miridae) (38). The enzyme profile of the omnivorous pentatomid bug *Podisus maeuliventris* is characterized, as expected from its mixed diets, by phosphatase, esterase, aminopeptidase, and carbohydrase (167).

Enzyme profiles cannot, however, serve as an unequivocal tool of food range recognition (167). For instance, the saliva of some mesophyll and seed feeders, such as *Oncopeltus fasciatus*, has been reported to contain proteases and lipases (62, 121). This is probably the result of an overlap between the enzymes required to digest components of different sources. Amylases, for example, hydrolyze starch, but they also digest polysaccharides such as glycogen and dextrines, which are found in animal cells (35, 102, 171). Some heteropterans considered primarily
phytophagous (e.g., *Lygus hesperus* and *L. lineolaris*) possess salivary pectinases and amylases that are indicative of plant consumption or even strict herbivory but also carry physiological elements, including in some cases venoms and phospholipases, distinctive of specialized carnivores (5, 36). The high incidence of omnivory in the Heteroptera may be related to their complex ingestion mechanism; their feeding includes strong elements of extra-oral enzymatic digestion, a process termed “solid-to-liquid feeding” (37, 38). It is possible that this highly developed tool, which allows for assimilation of nutrients beyond those readily available in plant fluids, provided this group with an advantage for plant tissue utilization.

Therefore only comprehensive analyses of both feeding behavior and enzymatic profile could provide accurate information. For example, tracking of radio-labeled isotopes from the plant showed that *Orius insidiosus* feeds primarily on the mesophyll and xylem, thus acquiring moisture and nutritional elements to supplement their prey diet (10). These findings were complemented by the demonstration of amylase in the saliva of this species (186). Nevertheless, some workers propose relying on the relative amounts of specific enzyme groups (i.e., proteases versus macerating enzymes such as pectinase and amylase) for placing a species on the zoophytophage-phytozoophage continuum (187).

**Behavioral Traits**

This section summarizes information on omnivores’ sensory needs for acquiring and processing gustatory information and the behavioral responses to those stimuli.

**NEUROSENSORY REQUIREMENTS** Feeding habits may be determined by the capacity to recognize food materials, which is based on the sensory repertoire of the consumer. Sense receptors of visual, chemical, and mechanical cues act at each step of food location and acquisition (e.g., 69). These cues were used to predict modes of feeding and nutritional adaptations of organisms (157). For example, visual cues are important in several predatory coccinellid species, but less so in *Coleomegilla maculata*, a phenomenon attributable to its omnivorous feeding habits (86). Some predators possess the neuronal infrastructure necessary to recognize plant materials as food. The generalist stinkbug *Eocanthecona furcellata* is attracted to (E)-phytol, a chlorophyll derivative that triggers proboscis extension, a characteristic response to a feeding stimulus (183). Similarly, different species of omnivorous grasshoppers quickly respond to proteinaceous animal food sources and are attracted to the food source, at least partially, using olfactory cues (180).

Neurological attributes of attentiveness, information processing, and decision-making mechanisms have been discussed intensively in recent years (14–16, 54). These reports demonstrate neurophysiological constraints particularly relevant for polyphagous herbivores that need to process large and complex sets of information. Because of a high degree of variability in the quality of host plants, compared with prey items, herbivores may be confronted with a more difficult task during food selection, compared with carnivores. Carnivores are thought to be limited
mainly by the rate of prey capture and handling time (72, 89). Omnivores probably face complexity similar to that faced by polyphagous herbivores. It is expected, therefore, that learning abilities in omnivores will be linked to nutritional balance, as was found in herbivores (107, 158). In fact, the capacity to recognize and associate specific odors with nutrients has been reported for the omnivorous cockroach *Periplaneta americana*, which is attracted differentially to various nutrients absent from its diet (72). Yet both *P. americana* and the herbivorous grasshopper *Locusta migratoria* could associate artificial odors with proteins but not with carbohydrates (72, 158). Further comparison of the two species showed that the omnivore exhibited faster learning and longer information retention than the herbivore.

FORAGING FOR DIFFERENT FOOD TYPES Most models that are derived from optimal foraging theory (168) consider only prey encounter rate when predicting patch selection and leaving by natural enemies. For example, the marginal value theorem predicts that a forager should leave a patch when its energy extraction rate is equal to the maximum average rate attainable for that environment as a whole (29). For omnivores, therefore, energetic budgets must include all potential food sources in the habitat, plants included. In this section, we discuss between- and within-habitat movement of omnivores in quest for food and their switching behavior between plant and prey resources.

Milne & Walter (122) suggested that *Frankliniella schultzei* thrips move into cotton fields to feed on mite eggs when high-quality food plants are not available. In contrast, Wilson et al. (182) reported that *Frankliniella occidentalis* does not actively seek prey but feeds on prey only as a result of random encounters on the leaf surface. Adults of the omnivorous heteropteran species *Geocoris punctipes* are more likely to remain on bean plants with pods than on podless plants. When pods are available, they spend considerable time feeding on them and thus not searching for prey (57, 59). Likewise, the coccinellid *C. maculata* was much slower to leave aphid-free corn plants and was less cannibalistic compared with other strictly predaceous ladybeetle species (154). Because the ephemeral nature of aphid prey populations forces aphidophagous coccinellids to change habitats rapidly and often, the lower dispersal tendency of *C. maculata* is related to its omnivorous feeding habits (161). Therefore omnivores may aggregate in response to changes in the abundance of both plant and prey food sources.

Once in the habitat, omnivores often face a choice between feeding on prey or on plant resources. *F. schultzei* larvae showed no preference for prey (spider mite eggs) over pollen, but in the field predation may occur primarily when pollen is not available (122). The western flower thrips, *F. occidentalis*, showed increased predation and decreased herbivory on mite-induced resistant cotton plants (4). Likewise, nymphs of the herbivorous grasshopper *Taeniopoda eques* shift to predation when plant availability declines in the habitat, thus allowing them to complete development and reproduction before winter frosts occur (180).

Behavioral constraints may alter the proportion of prey and plant material in the diet. For example, young spiderlings are apparently better at capturing and
feeding on aerial plankton, such as pollen and fungus spores, than they are at subduing insect prey (162). Likewise, herbivorous neonates may be unable to obtain water from sclerophytic plant tissues and thus feed on undefended arthropod eggs (180). Differences in the ability to find and use pollen, and thus in the degree of omnivory, were found in a comparative study of two omnivorous phytoseiid mites (174): *Iphiseius degenerans* aggregates in flowers to feed on pollen, whereas *Neoseiulus cucumeris* feeds on pollen deposits while foraging on leaves. In some cases, active pursuit of prey by an herbivore can be aggressive; a *Melanoplus foedus* grasshopper was observed to feed on a prey still impaled on the proboscis of its robber fly capturer (105). The use of legs (whether raptorial or not) during feeding is practiced primarily when mobile prey are being consumed. For example, the omnivorous thrips *Frankliniorthrips vespiformis* handles prey with the forelegs, but the legs are not used when feeding on plants (M. Guershon, personal observations). Omnivores may handle differently plant and prey items of a similar size and shape. Phytoseiid mites cut the cuticle of prey items with the penetrating chelicerae, then partially introduce the corniculi, and suck prey fluids with expansion-contraction movements of the pharyngeal muscles. Pollen grains, in contrast, are not cut, but they are picked up individually with one of the chelicerae. Then, alternate movements of the chelicerae rupture the grain exine, and the withdrawn contents are sucked up (64). Clearly, more detailed behavioral studies are needed to realistically apply optimal foraging theory to omnivorous species.

**Phylogenetic Traits**

Omnivory in arthropods could have evolved under different scenarios—as a primary condition evolving toward either carnivory or herbivory, as the transitional link between these two feeding habits, or as a derived state of either case. As a rule, carnivorous habits are considered to have arisen secondarily from phytophagous and scavenging ancestors, often through cannibalism (82). Indeed various species from taxa such as Orthoptera, Diptera, Coleoptera, and Lepidoptera are considered to have secondarily evolved from herbivorous to omnivorous and/or carnivorous habits (82, 95; and a review in 180). This evolutionary pathway is supported by a weak correlation found between degree of omnivory and taxonomic distance (e.g., 109). Yet other studies advocate other evolutionary pathways. In Dictyoptera, two evolutionary trends are commonly cited—the mantids remained carnivorous, whereas the cockroaches evolved to become omnivorous-saprophagous (75, p. 41). This shift to omnivory is thought to have occurred following opportunistic nitrogen scavenging in N-impoverished habitats (33). The observed omnivorous habits of some mantid species (143) have led to the suggestion to revise the taxonomy of the Mantodea. This suggestion must be treated with caution because these habits were recorded under unnatural conditions.

The original feeding habits of the Heteroptera have been controversial. Cobben’s (31) conclusion of carnivorous precedence has been challenged (170), rebutted (32, 156), and reendorsed recently (153). Nonetheless, it appears as if many groups
within the Heteroptera have reverted secondarily to omnivory or carnivory (36, 153). McMurtry & Croft (118) postulated that omnivory was the ancestral feeding habit of the phytoseiid mites. That omnivory is the primitive state was suggested also in a comparative study on mouthpart morphology of coccinellids (123). Recently, however, a carnivorous ancestral state was proposed for this group, with some species evolving to omnivory by adding nonanimal items, such as pollen, leaves, and fungi, to their diet (see 161 and references therein). It has been suggested that ancestors of current omnivores that rely on nectar for carbohydrate balance, such as blood-sucking Diptera, exploited the honeydew secreted by early homopteroids feeding on early plants (53).

It seems therefore that omnivory has appeared independently in different groups, at different times and through different evolutionary pathways, supporting the idea that evolutionary “trophic switching” is involved in the origins of this feeding habit (36).

ECOLOGICAL ATTRIBUTES OF OMNIVORY

Individual Level Processes

BENEFITS AND COSTS OF OMNIVORY The ability to exploit both plant and prey resources may benefit omnivores in several ways. We briefly discuss these potential benefits, some of which were similarly proposed for generalist herbivores, and we attempt to apply them here for omnivores.

The first obvious benefit of omnivory is a nutritional one. It is important, however, to distinguish between complementary and supplementary food sources (145). Complementing a vegetarian diet with prey, or a carnivorous one with plant material, may provide the omnivore with nutrients, vitamins, and minerals that are limited in its primary diet (27). Supplementary foods, by contrast, may substitute for each other, if only for relatively short periods. Most studies on diet mixing in generalist insect herbivores could not show consistent enhancement of fitness from mixed compared with the best single food (17; but see 18). This apparently is not the case for omnivores whether prey diet is supplemented with plant material or vice versa. In omnivorous heteropterans, for example, supplementing a plant diet with prey resulted in enhanced fitness in about 90% of the cases (40). Similarly, Whitman et al. (180) reported that supplementing a plant diet with various prey items had a strong positive effect on the reproduction of the lubber grasshopper, *Taeniopoda eques*. Some of the enhancement of omnivore fitness may be due to synergistic effect of plant and prey feeding. For example, a number of insect species, including termites, siricid woodwasps, and cerambycid xylophagous beetles, digest cellulose using fungal enzymes acquired while ingesting fungi along with their food (99, 100, 113).

By comparing the nutritional value of plant and prey foods, it is easy to understand how occasional consumption of prey could benefit herbivores. Plant foliage is of low nutritional value compared with insect tissues; protein content, for
example, is $2.8 \pm 0.6$ versus $17.7 \pm 1.4\%$ of fresh weight (data from Table 1 & 2 in 180), respectively. Plant tissues are also characterized by high levels of nondigestible materials such as lignin and cellulose. It is less apparent how predators benefit nutritionally by feeding on plant materials. Yet, in heteropterans, supplementing prey diet with plant materials enhanced longevity, development, and fecundity in about 60% of the cases (40). In some instances, water acquisition from tomato plants was required for the predatory mirid *Dicyphus hesperus* to complete its development on moth eggs (74). Further, zoophytophagous omnivores generally seek plant resources, such as pollen and seeds, that are of high nutritional value; the protein content of pollen, for example, was estimated to be 16–30% of fresh weight (180) and up to 61% dry weight (151). In hematophagous species that feed on a sugar-poor diet, intake of carbohydrates is important to sustain daily activities such as flight, and for overwintering survival (185).

The adaptive benefit of plant feeding by zoophytophagous species must also be assessed in view of the rapid spatial and temporal changes that commonly occur in prey availability. It is widely accepted that one of the main values of omnivory is that omnivores are able to persist in a habitat when one type of food source becomes scarce or its quality deteriorates. In many systems nectar feeding enhances the performance of carnivorous species during times of food stress (e.g., 24, 108, 129, 185). However, survival of zoophytophages that endure periods of prey scarcity by feeding on plants is usually lower than that of individuals feeding consistently on prey (e.g., 57). Often, plant feeding enhances omnivore survival but not reproduction, probably because water provisioning is crucial for survival, whereas the low nitrogen content of plant material retards egg production (49).

Moreover, inferior larval diet has a negative effect not only on larval performance, but on the adult stage, as well. The negative effects on adult fecundity are often irreversible and cannot be completely remedied by a high-quality adult diet. For example, the damage caused to *F. schultzei* nymphs by a diet of nitrogen-poor cotton leaves was not completely ameliorated by providing adults with prey (122). Yet the magnitude of these effects depends on the duration of prey deprivation and on the nutritional quality of prey and plants.

According to the diet-mixing hypothesis, the addition of plant material to the diet of predators should allow the dilution of any adverse effect of allelochemicals in the prey. However, Weiser & Stamp (177) could not find such alleviation of allelochemical effects in the omnivorous pentatomid bug, *Podisus maculiventris*. Conversely, herbivores that are well adapted to negotiate secondary plant compounds could feed on chemically defended prey. This is apparently the case with the grasshopper *Chrotogonus tachypterus*, which consumes cardenolide-defended larvae of the monarch butterfly (Siddiqui & Akbar 1966, cited in 180).

The value of a particular plant or prey resource is not constant and not independent of other foods; the value changes depending on environmental conditions (such as resource availability and quality) and on previously consumed items. For example, the benefit gained by *Géocoris punctipes* from feeding on bean pods is higher if the bugs prey upon poor-quality aphids than on nutritious moth eggs
Moreover, in some cases, supplementing a prey diet with plant material may negatively affect the performance of omnivores (47, 97, 177; and references in 45). It may be, therefore, maladaptive for zoophytophagous species to feed on plants when prey are abundant (177).

A reduction in interspecific competition may be another advantage of omnivory (83). Phytozoophages could move away from their host plant to feed on prey when density of herbivorous competitors is high. Similarly, zoophytophages could avoid competitors and their own enemies by feeding on plant resources away from aggregations of prey; more intense predation sometimes occurs in prey patches because enemies tend to aggregate there. Better yet, feeding on other guild members, be they herbivores or predators (i.e., exhibit intraguild predation), would act directly to reduce competition. Thrips, for example, facultatively feed on the eggs of their spider mite competitors (4). Omnivores that are engaged in reciprocal intra- or interguild predation with other predators (when both omnivore and predator species consume each other), directly remove their own enemies. For example, aphid herbivores reduce predation pressure by attacking and feeding on the susceptible egg stage of their coccinellid predators (Girault 1908, cited in 180).

Omnivory may also enhance the fitness of herbivores by shortening their developmental time, thus reducing their vulnerability to predation—by allowing herbivores to avoid feeding on defended host plants (3, 4) [similar to the toxin dilution effect suggested for herbivores (68)]; by lessening cannibalism and intraguild predation (46); and by reducing the searching cost when prey are rare (after 178).

Predation by herbivores may also entail significant costs. These omnivores may be injured or even killed in their attempt to subdue prey. The risk of injury may force herbivores to feed on small, undefended, weak, or sick prey. However, consumption of diseased prey may foster epizoonoses when omnivores ingest transmittable pathogens and parasites. Finally, prey may prove to be of little net energetic value if omnivores are inefficient predators, incurring high costs in pursuing, capturing, and consuming prey. Predators, on the other hand, may expose themselves to toxic secondary compounds when feeding on plant materials. For example, performance of fifth instar *Podisus maculiventris* declined when fed tomato plants (177).

Thus, a dynamic balance between costs and benefits probably governs the development and maintenance of omnivory. Herbivores may include prey in their diet according to nutritional requirements or in order to dilute any ingested poisonous plant chemicals, whereas predators may utilize plant resources to persist in habitats with prey shortage.

**PREY AND HOST PLANT SPECIFICITY** It is widely accepted that omnivores are the “ultimate generalists”—they feed on resources that belong to different phyla. Moreover, it is argued that herbivores with a narrow range of host plants should not be olfactorily and gustatorily equipped to respond to prey items. Thus, monophagous herbivores that consume prey are expected to do so only because the prey are contaminated by the odor of the herbivore’s food plant (180).
OMNIVORY IN TERRESTRIAL ARTHROPODS

Nonetheless, some omnivores do feed on rather specific resources. The habitat specialist colydiid beetle *Lasconotos subcostulatus* supplements its fungal diet with bark beetle larvae, with which it shares galleries (80). Larvae of the specialist geometrid *Prochoerodes truxaliata* readily feed on young midge larvae (149). *Anthocoris nemoralis*, an omnivorous bug, enjoys increased fitness as a result of feeding on young leaves and pollen of various tree species (L. Shaltiel & M. Coll, unpublished data). As a predator, however, it preferentially feeds on psylla nymphs (88). Omnivores may also feed preferentially on a particular type of prey, for instance prey of high mobility, even if it is not the most suitable one (58). Finally, many other carnivorous arthropods feed specifically on pollen and thus are found primarily on pollen-producing plants (e.g., predatory thrips, anthocorid, and mite species).

We need to keep in mind, however, that omnivorous species, like generalist herbivores (67), may be made up of populations that differ in their diet repertoire. Each population may exhibit a different degree of plant and prey mixing and different levels of plant and prey specificity.

**Population Level Processes**

Until recently, most theoretical and empirical studies of omnivory have focused on systems where the omnivore feeds on several prey items, primarily in aquatic systems. In these studies of trophic omnivory, the relative size and abundance of the different prey items are thought to determine their relative consumption (50, 140, 141). Because true omnivores rely on vastly different food sources, prey and plants, their population dynamics are expected to differ greatly from those of other trophic omnivores (135).

**OMNIVORE-PLANT ASSOCIATION**

Much like herbivores, omnivorous species are strongly affected by nutritional, allelochemical, and morphological characteristics of their host plants (see reviews in 39, 180). For example, dense leaf hairs prevented *Orius insidiosus* bugs from feeding on soybean leaves. These bugs suffered decreased longevity on plants severely infected with soybean mosaic virus and had higher longevity on young and old than on mid-aged soybean leaves (11). Omnivores, like many herbivores, may prefer to oviposit on plants more suitable for offspring development (39). Yet, host preference was not always correlated with larval performance; *O. insidiosus* females preferred to deposit their eggs into tissues of pepper plants, but the emerging nymphs showed low performance on pepper foliage (39).

It has been suggested that plants may recruit bodyguards in the form of predators and parasitoids as a defense strategy (176, 179). These enemies attack herbivores that feed on the plants. A major mean of attracting natural enemies is by the provisioning of food sources. Plants supply omnivores with floral and extrafloral nectar, pollen, and ant food-bodies to gain protection from herbivores (179). Many omnivores, including coccinellids, syrphids, ants, tachinids, and parasitic wasps,
are attracted to and feed on these resources, and thereby maintain large populations on plants that provide special foods; these omnivores may then prey on the herbivores found on their host plants. Thus, strong direct effects of high-quality plant resources on omnivores may result in a trophic cascade that would benefit the plants (Figure 2c). However, the impact of omnivores on plants depends on the relative strength of interactions between consumers in the system (165).

OMNIVORE-PREY DYNAMICS  Omnivores often attain higher population densities in habitats containing superior plant foods, such as pollen, seeds and fruits, compared with habitats without these materials (46, 57, 85). Feeding on such plant materials often increases omnivore population density not only through local aggregation but also because it enhances reproduction and decreases mortality of the omnivores, and thus leads to faster population buildup. For instance, adult *Orius* bugs are attracted to pollen-producing plants, where they colonize the flowers (172a) and plant parts where pollen accumulates (e.g., corn leaf axils) (42), and *Orius* bugs enjoy increased performance when prey diet is supplemented with pollen (34). For *Orius* and other species (e.g., *C. maculata*), where habitat preference is linked to their pollenivorous habits (42, 60), flower abundance is a good predictor of omnivore population density. In *G. punctipes*, in contrast, density of bean pods, rather than flower or prey density, was a good predictor of population size (57). Prey density was a good predictor of the abundance of strictly predatory species in the system; their density was similar in bean plots with and without pods (57).

High omnivore densities do not necessarily lead to greater suppression of prey populations. Cottrell & Yeargan (46), for example, found lower predation rates of *Helicoverpa zea* eggs in the presence of corn pollen than in its absence; yet Coll & Bottrell (unpublished data), working in a similar corn system, found higher predation on *Ostrinia nubilalis* eggs in plots with pollen than in no-pollen plots. Eubanks & Denno (57) showed that *Geocoris punctipes* populations were larger and suppressed prey populations more effectively in pod-bearing bean plots compared with podless plots, although predation rate per individual bug was lower in the presence of pods than in their absence (59). A similar reduction in predator efficiency but longer tenure time and higher overall predation was found in alfalfa plots in the presence of pollen-providing dandelions (85). The direct positive effects of plant feeding (increased survival and decreased emigration of omnivores)

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**Figure 2**  Direct (solid arrows) and indirect (dashed arrows) effects of interactions in a three-species system that includes an omnivore that feeds on the plant and the herbivore in the system. (a) Resource competition, (b) facilitation/impediment, and (c) trophic cascade are depicted. Note that resource competition is important for phytozoophagous omnivores, whereas trophic cascade occurs for zoophytophagous omnivores but not for phytozoophagous ones. The thickness of the solid arrows represents the relative intensity of the effect, and the nature of the indirect effects (positive or negative) is given in parentheses.
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a) Resource competition

b) Facilitation/Impediment

c) Trophic cascade
sometimes override direct and indirect effects of plant resources on prey populations (enhanced prey performance on superior plant food and decreased predation while omnivores feed on plants).

Taken together, empirical and theoretical studies suggest that feeding on both plant and prey resources should allow omnivores to persist at low prey densities and thus decouples the dynamics of omnivore and prey populations. Yet the overall effect of plant feeding on herbivore population suppression depends on factors such as prey and plant nutritional qualities, duration of prey scarcity, prey mobility (for visually searching omnivores), and the role neighboring habitats play as sources for colonizers. Also, the relative rate of prey consumption differs for male and female omnivores, probably because of different nutritional needs (e.g., 98). Many zoophytophages tend to be phytophagous in their early instars and feed on both plant and prey resources only at later stages (e.g., 30, 163). In these cases, the dynamics of the interaction would differ from those predicted by predator-prey or competition theory alone (127). Competitive interactions between omnivores and prey, such as an omnivore-induced niche shift by the prey (44, 140), may also strongly influence their population dynamics. Therefore, it is unlikely that a broad generalization, such as the suggestion that omnivores are better than strict predators in prey population suppression, could be strongly supported at this stage of our mechanistic understanding of these interactions.

Community Level Processes

OMNIVORY AND OTHER HIGH-ORDER COMPLEX INTERACTIONS Some interactions described for trophic omnivores (e.g., 141, 50) may be similarly applicable to systems with true omnivores; others are not applicable or may apply in a different manner. Let us examine some direct and indirect interactions in the simplest food web that includes an omnivore. This system involves an omnivore, an herbivorous prey species and a plant resource common to the two consumers (Figure 2). When plant resources are limited, exploitation competition may occur between a phytozoophagous omnivore and the herbivore in the system (Figure 2a). Such competition may be asymmetrical, favoring the herbivore because it is likely to be more effective in plant utilization. Zoophytophagous omnivores, however, may monopolize plant resources in a given system because they prey heavily on their herbivorous competitors. This appeared to be the case when O. insidiosus displaced thrips from their preferred feeding sites on pepper and bean plants (44). For zoophytophages, therefore, the indirect competitive effect is expected to be relatively minor compared with the direct predatory effect.

Omnivory may produce indirect facilitation or impediment effects on the plant and the herbivore (Figure 2b). Feeding on plants by phytozoophagous omnivores may reduce plant consumption by the herbivore, for example through the induction of resistance traits. In other cases, phytophagy may weaken the plants, thus making them more susceptible to attack by herbivores. Likewise, zoophytophagous omnivores may displace herbivores from preferred feeding sites and indirectly benefit
or harm the plants, depending on the relative damage inflicted by the herbivore during feeding at different sites on the plant. This type of facilitation and impediment effects are unique to systems with true omnivory. Apparent competition may occur in similar configurations with trophic omnivory.

Finally, a zoophytophagous omnivore may cause a trophic cascade (i.e., indirectly reduce plant damage) primarily through direct predation on the herbivore (Figure 2c). No indirect effects are expected to occur between phytozoophagous omnivores and their host plants.

A few studies elucidate more complex interactions. Agrawal et al. (4) and Agrawal & Klein (3) studied complex direct and indirect effects of induced plant resistance on an omnivorous thrips. They found that a decrease in plant suitability resulted in a shift toward more predation by the omnivore. However, resistant plants also affect the density and quality of mites on which the omnivore feeds (22). In turn, the decrease in prey density and quality reduces thrips consumption rate and thus counteracts the shift to predation (3). The relatively low level of aggressiveness in *C. maculata* attributed to its omnivorous feeding habits, resulted in high predation by lacewing larvae [i.e., a high degree of asymmetrical intraguild predation (110, 111, 131)]. Also, a lower cannibalism rate was recorded in this species compared with other, strictly predaceous ladybeetle species (154). On the other hand, omnivory may be viewed as a strategy to reduce levels of intraguild predation (and cannibalism); it allows omnivores to change their location and feed on plants in the presence of other predators. In agreement with this idea, Cottrell & Yeargan (46) found that egg cannibalism by *C. maculata* was lower in the presence than in the absence of corn pollen. It is clear that the relative significance of these complex interactions will vary with the particular characteristics of the food web. For example, predation pressure experienced by a herbivore may be alleviated when its omnivorous natural enemy also feeds on other prey species on other host plants (see review in 90) or feeds directly on other host plants (integuild omnivory) (Figure 1d).

The Hairston, Smith and Slobodkin (HSS) hypothesis (84, 160) predicts that top-down cascades among trophic levels determine the structure of ecological communities. However, trophic omnivory (and true omnivory) is ubiquitous in nature and apparently acts to diffuse the strength of predation. Thus, systems with omnivores may no longer be recipient controlled, where carnivores exert strong effects on prey populations, but these systems may instead be donor controlled, with prey influencing consumer dynamics. If so, trophic cascades may not be expected in webs that include omnivorous species (138).

**STABILITY OF COMMUNITIES WITH OMNIVORES** The idea that complex food webs, with many connections between species, omnivory, and long food chains, are unstable, although counterintuitive, dominated the ecological literature for nearly two decades. Complex systems were thought to have a poor ability to recover from perturbations and thus to have disappeared. It is now clear, however, that complex webs are stable and do exist. The many links that connect species in the community tend to dampen population fluctuations and stabilize the system (116, 139).
On theoretical grounds, omnivory was expected to be rare in natural systems because it supposedly places the prey in double jeopardy because the intraguild omnivore is a predator and a competitor for shared resources (the plants) (135; Figure 1). In their seminal paper, Pimm & Lawton (135) used simple models to test the stability of food webs that include trophic omnivores. They found that (trophic) omnivory destabilizes food webs. For several reasons this finding has been reevaluated: (a) Omnivory is common in a variety of natural food webs and (b) recent theoretical analyses of trophic relationships have revealed that omnivory can increase stability in food webs, particularly when the interactions are not too strong (61, 91, 106, 115).

However, these studies modeled trophic omnivory in general. To date, only two theoretical studies (44, 103) have attempted to model specifically the dynamics of true omnivores and their prey. These studies were aimed at reconciling the apparent contradiction between Pimm & Lawton’s (135) prediction that omnivory destabilizes ecological systems and the increased realization that omnivory is common in nature. In their initial exploration of omnivore-prey systems, Coll & Izraylevich (44) showed that, under certain conditions, plant feeding indeed has a destabilizing effect on systems that include plant-feeding omnivores, both through uncoupling of predator-prey population dynamics and through the effect of competitive interactions. Lalonde et al. (103) expanded on this first analysis and found that these systems were stable at a narrow intermediate level of omnivory but were rapidly destabilized as the omnivore behaved more like a strict carnivore or a strict herbivore. Thus, switching between plant and prey feeding provides a refuge for the prey when it is at low densities. Another factor that may stabilize the system is the relatively poor searching efficiency of the omnivore (103). Thus, even high levels of omnivory may be stable because the omnivore is not effective in prey exploitation.

Several other properties of food webs with omnivores may have a stabilizing effect. Feeding at more than one trophic level may effectively shorten food chains, thereby promoting their persistence (166). In many long-food-chained marine and aquatic systems, omnivores near the top of the food chain derive much of their energetic needs from organisms that occupy trophic levels near the bottom of the chain. Functionally short chains are believed to be more stable than longer ones (133). The second property suggested to increase community stability is “life history omnivory” (omnivores that feed at different trophic levels as they mature). This type of omnivory may be stabilized by the release in predation pressure at different life stages (136).

When two or more asynchronous multivoltine omnivorous species cooccur, the simultaneous presence of small undefended juveniles together with larger adults may lead to complex double-trophic omnivory. In such systems, the omnivores feed on each other to show intraguild predation, and they also feed on herbivores with which they share common host plants. Similar types of reciprocal predation are thought to have a stabilizing effect on community dynamics (133). Such complex interactions are not uncommon. For example, many omnivorous heteropterans
are also engaged in intraguild predation (149, 150, 155). However, the nature of direct and indirect interactions in such systems is poorly understood. Finally, self-limiting processes such as asymmetrical omnivore-prey competition may also lead to stability (184).

In general, a balance between the omnivore’s predation rate and the superior ability of the herbivore to exploit plants may sustain systems that include omnivorous closed loops. Omnivory can potentially buffer the effects that outbreaks or rapid declines in prey populations may inflict on food webs. Thus, it may reduce the impact of disturbances and promote food web stability.

APPLIED CONSIDERATIONS OF OMNIVORY

Crop Damage

The beneficial value of an omnivore that preys on and competes with pest species may be counteracted by any economic damage it may inflict as an herbivore. In fact, the predatory and pestiferous status of many omnivores is often confused (see examples in 40). The mirid *Dicyphus tamaninii* effectively controlled whiteflies and thrips in cucumbers and was not found to damage the fruit (70). In tomatoes, however, this omnivore inflicts significant fruit damage when high predator populations coincide with low whitefly (prey) densities (7, 71). Careful monitoring of both pest and omnivore populations and use of decision making tools for omnivore release or chemical control, based on predator-to-prey ratios (7), may permit use of this omnivore in affected crops (112). In contrast, the congeneric *D. hesperus* prefers feeding on tomato leaves over fruits and therefore may be more suitable for whitefly and spider-mite control in this crop (117). Furthermore, some omnivorous nabids have been implicated as vectors of plant fungal pathogens (25). Clearly, there is a need to carefully assess the benefit gained by omnivorous species acting as predators against any damage they may cause as plant feeders (98).

Biological Control

Theoretical explorations suggest that omnivory stabilizes herbivore populations only when it coincides with high population densities of the prey (103). Thus, biological control efforts that deploy omnivorous species should be augmentative and should not expect stability of the system. In view of the generalist feeding habits of most omnivores, their use in biological pest control should be carefully assessed; they may attack nontarget herbivorous and predaceous prey, disrupting natural as well as agricultural ecosystems. Further, in biocontrol programs of weeds, herbivores introduced to control an invading weed may show omnivorous habits and also feed on other herbivores, thus hampering control efforts (see examples in 149). In contrast, host feeding by parasitoids may greatly enhance pest population suppression; in some species, the impact of host feeding on host populations may
be far greater than that of parasitism (48, 172 and references therein). Likewise, the ability of omnivores to sustain populations on plant resources when prey densities are low may result in more effective pest control. For example, a single seasonal release of *Orius* spp. is sufficient to control thrips in a pollen-producing crop such as sweet pepper, whereas at least two releases are needed in crops without pollen (173).

Plant resources may be used in the rearing and delivery of omnivores in augmentative biocontrol programs. Plant materials provide omnivores with important nutrients and moisture, particularly when the young instars are not predaceous (e.g., 19, 128). For example, the addition of plant material to a prey-only diet enhances survival, shortens development, and increases reproduction in most predatory Heteroptera (45 and references therein). An open rearing system that consists of potted pollen-producing *Ricinus communis* plants is used to rear and field-introduce the omnivorous mite *Iphiseius degenerans* for thrips control in sweet pepper (144). Finally, plant materials should be considered in our continuing attempts to develop suitable artificial diets for mass rearing of omnivorous biological control agents (e.g., 79).

Conservation of naturally occurring omnivores is desirable because they may persist in the habitat at low prey densities, thus impeding any buildup of pest populations. The presence of high-quality plant resources, such as pollen and nectar, may be a good predictor of the abundance of omnivorous parasitoids and predators, and thus for potential suppression of pest populations (e.g., 1, 94, 104, 179 and references therein). In “clean cultures” required plant food sources may be unavailable for omnivores, thus forcing them to leave the habitat. Tolerance for weeds in the field and manipulation of vegetation within and near cropland may help retain and sustain omnivores in the field (40, 41, 104 and references therein). However, little movement of omnivores onto crop plants is expected if weeds flower throughout the growing season and provide ample pollen and nectar. Regular cutting of weeds may be needed when pest populations increase in the field (130). In another approach, food sprays consisting of various formulations of sugars and yeast hydrolysates were tested with limited success in several cropping systems; in general, higher densities of omnivorous natural enemies in treated fields did not necessarily lead to pest suppression (81, 120). Obrycki & Kring (126) nevertheless recommended further work on this approach.

**Chemical Control**

To their detriment, omnivorous species may be exposed through direct feeding to systemic pesticides (12, 23, 56, 148). For example, the coccinellid beetle *C. maculata* showed lower mobility, decreased survival, and a longer preoviposition period on inflorescences of plants treated with the systemic insecticide imidacloprid than on untreated plants (164).

Omnivores may exhibit higher levels of insecticide resistance than do pure carnivores for two reasons. First, if species that feed on plants have a greater array of
detoxifying enzymes than do predatory species (76), it is expected that omnivorous species will be better able to deal with toxic secondary plant compounds compared with other natural enemies. This prediction may be supported by the higher levels of genetic polymorphism in esterases found in omnivorous than in predaceous mites (26). The second characteristic that may influence the rate at which omnivores evolve insecticide resistance is their apparently low tendency to disperse when prey density declines. Thus, compared with pure carnivores, omnivores should have a lower level of gene mixing acting to dilute the selective effect of pesticides (43). It would be interesting to test these predictions experimentally and through a literature survey.

**Cultural Control**

Recent work demonstrates that plant resistance traits may directly affect omnivorous natural enemies. Agrawal (2) suggested that induced resistance may be a particularly useful strategy because it reduces herbivorous pest populations both directly (through, for example, toxic effects) and indirectly by causing a shift toward predation in naturally occurring omnivores. Moreover, Bottrell et al. (20) suggested that crops could be bred to accommodate the nutritional needs of natural enemies.

A few studies have examined the direct effect of feeding on genetically engineered plants on omnivores. For example, no acute effects were detected when omnivorous species were fed Bt-expressing corn pollen or potato foliage (132). The salivary and intestinal proteinases that omnivores possess may enable them to inactivate toxic proteins (9). Yet newly developed transgenic crops, such as those that confer resistance to homopteran pests (e.g., snowdrop lectin), may prove to have a more pronounced negative effect on omnivorous heteropterans.

Several cultural practices may also influence omnivores. Irrigation (i.e., water stressing) and nitrogen fertilization, which both alter plant nutritional value for pests, may similarly affect omnivorous insects (11, 78; M. Guershon, R. Groeneman & M. Coll, manuscript in preparation). Harvesting whole ornamental plants or flowers in cut-flower crops may dramatically reduce the population density of pollen-feeding omnivores, whereas pruning and the resulting flush growth may enhance activity of leaf-feeding omnivores (77).

**CONCLUSIONS AND SUGGESTIONS FOR FUTURE WORK**

This review illustrates that omnivory is a highly complex phenomenon. This complexity occurs at both the individual and community levels. Because omnivores have a particularly wide range of plant and prey items to choose from, the challenge for ecologists is to understand the factors that shape a particular diet mix exhibited in nature. Attempts to do so in omnivorous vertebrates have been, for the most part, unsuccessful probably because under highly complex and variable conditions, the optimal strategy is too complex for the animals to use (13). This may also be the
case for omnivorous insects; neurophysiological, biochemical, and phylogenetic constraints may prevent optimal diet mixing.

The highly complex interactions found in ecological systems that include omnivory—due to various configurations of predatory and competitive effects that occur at different times and places—affect the dynamics, resource utilization, and demography of interacting populations. These in turn influence the structure and function of food webs. Much empirical and theoretical work is needed to untangle the complex nature of these systems. Mechanistic understanding of underlying physiological, behavioral, and ecological processes is needed in order to assess omnivory in nature and gain insights to its possible evolutionary pathways. The deficiency in research effort is particularly apparent in natural systems.

Although switching between prey and plant feeding by omnivores is predicted to stabilize ecological systems, little is known about the factors that govern the switch between predation and plant feeding. Also, we reviewed several hypotheses on the adaptive function of plant and prey feeding by omnivores, but there is no evidence that any of these benefits actually occur in nature. To demonstrate benefit, we must assess the cost of maintaining any physiological, morphological, and/or behavioral traits that allow omnivory. Two approaches seem particularly rewarding for future studies. First, comparative studies that involve related species could test the relative effectiveness of omnivorous, carnivorous, and herbivorous species at resource utilization. Studies on coccinellids, mirids, thrips, and phytoseiid mites could thus characterize predatory behavior of zoophytophagous versus phytzoophagous insects and levels of cannibalism in herbivores (i.e., omnivory) versus carnivores (IGP) in the field. The second approach may be used to assess population interactions through independently manipulating omnivores, herbivores, and plant resources, for example, in large field cages. Such a setting could be used to test, for example, the usefulness of omnivory as a strategy to minimize intraguild predation and competition. In that respect, it would be interesting to determine whether omnivores serve as intraguild prey more often than carnivores because of their supposed lower level of aggressiveness.

The ubiquity of omnivory in both natural and managed ecosystems, as demonstrated in this review, urges us to reassess our view of food web structure. Trophic levels are hardly ever distinct; many organisms consume resources at different trophic levels, particularly plants and prey. This realization should alter our view of the way populations are regulated (HSS model) (84, 160) and of the factors that hinder biological control.

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