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Zoophytophagous Heteroptera: Implications for Life History and Integrated Pest Management

Phytophagy in Predaceous Heteroptera: Effects on Life History and Population Dynamics

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Predaceous heteropterans are among the most abundant species of predators in many agricultural systems. However, we have only a rudimentary understanding of the biology and ecology of these predators in crop ecosystems. The literature is replete with observations of plant-feeding by predaceous species, but the phenomenon has been studied in some detail in only certain groups of the Heteroptera. In general, phytophagy is considered an important factor in allowing predaceous heteropterans to colonize crops before the arrival of prey, and in permitting subsistence during other periods when prey are scarce. However, plant food also may represent an important complement to a carnivorous diet. We summarized a number of laboratory studies in which life-history traits of various predators were measured relative to diets containing prey and plant components. This analysis showed that the benefits of phytophagy are species-specific and are dependent on predator age and the quality of the prey and plant components of the diet. Available information suggests that anthocorids and mirids may be the only predaceous Heteroptera capable of fully substituting phytophagy for carnivory. For example, several Orius *spp. can develop and reproduce on plant food alone. Phytophagy alone can support limited development of predaceous species within the Lygaeidae and Pentatomidae, but only subsistence in species within the Nabidae and Reduviidae. Supplemental plant feeding may be essential for development and reproduction of predators feeding on low-quality prey, but may have only minor effects on the life history traits of predators feeding on* *high-quality prey such as insect eggs. However, even subtle differences in individual life-history parameters may produce significant changes in population level processes. Computer simulations of* Geocoris punctipes *(Say) life history suggested that even subtle plant feeding effects on nymphal development and survival and on adult oviposition may translate into dramatically higher rates of reproduction and predation. We also examined a number of studies that allowed an indirect evaluation of the significance of phytophagy in predaceous heteropterans. Although difficult to partition out the effects of reduced prey abundance, comparative studies of nectaried and nectariless cotton generally suggest that many species of predators are less abundant in nectariless cotton. Other plant association studies suggest that nectaries and other plant resources may increase the densities of certain species of predators, and observations of predator feeding behavior indicate that phytophagy is common in nature even in the presence of abundant prey. Studies of energetics, nutrition, and complete life histories, using realistic mixtures of prey and plant foods, will be needed to evaluate fully the importance of phytophagy in predaceous Heteroptera.*

The potential for predaceous arthropods to regulate populations of insect pests has been recognized for well over 100 yr (Whitcomb 1980). Predaceous members of Heteroptera are among the most numerous species in many agricultural systems, including cotton (Whitcomb and Bell 1964, Schuster et al. 1976, Ehler 1977, Henneberry et al. 1977, Stoltz and Stern 1978b, Wilson and Gutierrez 1980, Adjei-Maafo and Wilson 1983, Trichilo and Leigh 1986), soybeans (Barry 1973, Shepard et al. 1974, Whitcomb 1974, Deitz et al. 1976, Morrison et al. 1979, Irwin and Shepard 1980, Bechinski and Pedigo 1981, Lentz et al. 1983), corn (Barber 1936, Dicke and Jarvis 1962, Coll and Bottrell 1991, Reid 1991), alfalfa (Pimentel and Wheeler 1973, Benedict and Cothran 1975, Wheeler 1977, Braman and Yeargan 1990), various vegetables (Tamaki and Weeks 1972; Bugg and Wilson 1989; Bugg et al. 1991; Alomar and Albajes, this volume), and horticultural crops (Braimah et al. 1982; McCaffrey and Horsburgh 1986; Arnoldi et al. 1991; Reding and Beers, this volume; Thistlewood and Smith, this volume). Despite the extensive literature on predaceous Heteroptera, we still know little about how these generalist predators affect economically important pest insects (e.g., Whitcomb and Bell 1964, Barry et al. 1973, Ehler et al. 1973, Elvin et al. 1983, O'Neil 1988) and how features of their biology and ecology allow these predators to persist in agricultural systems.

Tritrophic studies concerning plant–herbivore–natural enemy interrelationships have become pervasive in the ecological and entomological literature (Van Emden 1965, Price et al. 1980, Boethel and Eikenbary 1986, Barbosa and Letourneau 1988) and will probably increase and improve the use of biological control in agroecosystems. Plants influence predators in a number of important ways (Price et al. 1980). Uncultivated plants may serve as refuges for alternative prey for predatory arthropods during and between cropping cycles (Van Emden 1965). Plants also may provide moisture and nutrients to predators when prey are scarce, and contribute important supplemental nutrients to a largely carnivorous diet.

Phytophagy is known to occur in a number of predator groups (e.g., Smith 1961, Hagen 1962, Yokoyama 1978, Kennett et al. 1979, Smith and Mommsen 1984, Ouyang et al. 1992); however, within the predaceous Heteroptera the use of a broad range of both plant and animal food resources appears to be widespread (Balduf 1939, Southwood and Leston 1959, Miller 1971, McPherson 1982, Henry and Froeschner 1988, Lattin et al. 1989, Dolling 1991). Some of the early literature hints at the confusion in distinguishing between herbivory and carnivory in this group. For instance, Watson (1931) reported *Geocoris punctipes* (Say) as a pest of lettuce in Florida, and Lockwood (1933) reported *Geocoris* spp. as destructive to cotton in California. A mirid, *Cyrtorhinus mundulus* (Bredd), was recorded as a pest in Java but was later found to be a highly effective predator of sugarcane leafhopper eggs (Debach 1974). Conversely, true bugs known to be pests have been observed feeding on other insects. For instance, Dunbar and Bacon (1972) observed *Lygus hesperus* Knight feeding on *G. punctipes* nymphs, and recent studies show that *L. hesperus* is one of the most frequent predators of eggs of *Bemisia tabaci* (Gennadius) and *Pectinophora gossypiella* (Saunders) (Hagler and Naranjo 1994). Similarly, the cotton fleahopper, *Pseudatomoscelis seriatus* (Reuter), preys on *Heliothis* spp. eggs in cotton (Agnew et al. 1982), and false chinch bugs, *Nysius* spp., have been observed preying on lepidopteran eggs in cantaloupes (Bugg et al. 1991). Plant feeding is prevalent even within families that contain only predaceous members (e.g., Nabidae, Reduviidae, and Phymatidae); however, phytophagy is best known in the Miridae and in the subfamilies Asopinae and Geocorinae that belong to the largely plant-feeding families of Pentatomidae and Lygaeidae, respectively. The key to using the biological control potential of predaceous heteropterans may lie in understanding the role of phytophagy.

The evolution of herbivory and carnivory within the Heteroptera is controversial. Cobben (1979) contended that carnivory was the ancestral lifestyle, whereas Sweet (1979) argued that ancestral forms were largely phytophagous. Regardless, the predominance and importance of carnivory within the Heteroptera is well established. Over half of all families in North America are predaceous (Henry and Froeschner 1988), and the predaceous life style apparently has arisen independently numerous times (Cohen 1990). Recent work suggests that predatory species representing both predaceous and seed-feeding families (Lygaeidae, Nabidae, and Reduviidae) are morphologically and physiologically equipped to feed on plants (Cohen 1990, this volume).

Phytophagy probably has contributed to the abundance of some groups of predaceous Heteroptera (Sweet 1960). Predators inhabiting many agricultural systems, particularly annual crops, face extreme temporal and spatial variation in prey abundance (Ehler and Miller 1978, O'Neil and Wiedenmann 1987, Wiedenmann and O'Neil 1990). Adaptations of species of predators that permit subsistence under such variable conditions underlie the success of these species in annual cropping systems. It has been suggested that certain predators have evolved prey-searching behaviors and life history strategies that permit them to survive and reproduce when prey are scarce (O'Neil and Wiedenmann 1987; Wiedenmann and O'Neil 1990, 1992). Phytophagy is probably an adaptive trait in such circumstances.

Scope of This Review

Herein, we summarize many studies to evaluate the importance of plant feeding in predaceous Heteroptera. We emphasize 2 major types of studies. First, we examine controlled studies in which life history characteristics were measured relative to diets containing prey and plant components. We include in this category studies in which plant or prey material was the sole nutrient source or in which plant and prey materials were supplemental to one another. Second, we indirectly evaluate the role of phytophagy by reviewing some observational studies, comparative studies of predator abundance in nectaried and nectariless cotton, and plant association studies. Studies of this type are widespread because of the difficulty in designing and conducting tritrophic level experiments (Letourneau 1988). Finally, we will suggest future areas for research. We will draw largely from work on predators common to annual crops. This is based partly on our greater familiarity and experience with field crops and partly on the bias of the literature which is heavily skewed to certain genera (notably *Geocoris* and *Orius*). Thus, this review is not comprehensive. In particular, we have not fully explored the Miridae, which is covered in more detail by other authors in this volume.

Finally, we feel that it is important to provide a working definition of plant feeding for the purposes of this review. Strong et al. (1984) rigidly defined phytophagous insects as those feeding on the living tissues of higher plants and implicitly excluded feeding on nectar and mature seeds. Because such resources are available to foraging predators in many habitats and may contribute to overall predator nutrition, we choose a broader definition of phytophagy that includes these derivative resources.

Effects of Plant Feeding on Life History Traits

The influence of phytophagy on life history traits has been examined in a relatively small number of species using a wide array of prey species and many different kinds of plant food. In this paper we classify the types of studies conducted as (1) prey diets supplemented with plant food, (2) plant diets supplemented with prey food, (3) water diets supplemented with plant food, and (4) comparisons of prey-only and plant-only diets. The first 2 categories permit evaluation of the complementary role of phytophagy in a predator's diet, whereas the last 2 categories allow analysis of whether, and to what degree, plant-feeding can be substituted for carnivory. In studies where a wide range of plant materials were examined (Stoner 1970, 1972; Stoner et al. 1974, 1975; Naranjo and Stimac 1985) we chose selective examples from the plant foods evaluated.

Supplemental Plant Feeding. In general, supplementing a diet of prey with plant food has a positive effect on nymphal and adult life history traits; however, the benefit of plant feeding depends on the type of prey and plant food, and is species- and developmental stage-specific (Table 1). For instance, supplementing prey (greenbugs, cotton aphids, thrips, or mites) with plant food decreased developmental times and increased survival rates of nymphal *Orius insidiosus* (Say), and generally increased adult fecundity and longevity. Conversely, plant supplements were generally less beneficial either to nymphal and adult *O. insidiosus* being fed *Heliothis virescens* (F.) eggs, or to nymphs of *Orius tristicolor* (White) feeding on thrips. Plant food is essential for nymphal development and reproduction of *Geocoris bullatus* (Say), *G. pallens* Stål, and *G. punctipes* on a diet of pea aphids. However, supplemental plant feeding is less important when these same species are offered any of various lepidopteran eggs (Table 1). Even so, fecundity and nymphal survival of *G. punctipes* feeding on lepidopteran eggs can be significantly increased by supplemental green bean or leaf sap. Plant food also is beneficial to the predatory mirid, *Campylomma livida* Reuter, even if *Heliothis* sp. eggs are offered as prey.

Although difficult to generalize, several points are noteworthy. Cohen and Debolt (1983) argued that because of the high nutritive quality of insect eggs as prey, plant-feeding by *G. punctipes* provides only essential moisture. This conclusion appears valid for *O. insidiosus* as well, but it does not apply to *G. punctipes* feeding on eggs of *Spodoptera frugiperda* (J. E. Smith) (Naranjo and Stimac 1985). Arguably, the benefits of plant-feeding are relatively minor with insect eggs as prey, but some predators can derive additional nutrients as well as moisture from feeding on plants. Another important point concerns the inconsistent results obtained with green beans. Kiman and Yeargan (1985) suggested that pesticide residues in commercially obtained green beans may have contributed to reduced nymphal survival of *O. insidiosus*, and Braman and Yeargan (1988) speculated that contaminated green beans led to inconsistent results in oviposition studies with *Nabis* spp. In retrospect, reduced nymphal survival in the study of Naranjo and Stimac (1985) also hints at problems with pesticide-contaminated green beans. The extent of the problem is probably variable, depending on sources of beans and preparation techniques. We should be aware of the

Table 1. Influence of supplementing various prey-only diets with plant food on selected life history traits of some predaceous heteropterans

Species	Prey food	Supplemental plant food	Nymph		Adult female			Reference
			Develop-ment time	Survival to adult	Fecundity	Longev-ity	Wt	
Anthocoridae								
Orius insidiosus	Greenbug	Green bean	–15.7*	–1.0	8.3	1.2	—	Bush et al. 1993
	Cotton aphid	Green bean	–15.9*	14.0	12.1	2.2	—	
	Heliothis eggs	Green bean	–9.1*	–1.0	43.1*	61.1*	—	
Orius insidiosus	Thrips	Pollen	–7.0	28.2*	89.7	–3.5	—	Kiman and Yeargan 1985
	Heliothis eggs	Pollen	0.7	–0.2	3.2	17.8	—	
	Mites	Pollen	–0.7	–3.0	8.1	–1.9	—	
	Thrips	Green bean	–5.1	8.9	3.4	9.8	—	
	Heliothis eggs	Green bean	4.5	–7.0	–0.8	6.7	—	
	Mites	Green bean	–0.7	–21.9*	–57.2	10.3	—	
Orius tristicolor	Thrips	Green bean	8.2*	7.5	—	—	—	Salas-Aguilar and Ehler 1977
	Thrips	Pollen	–10.6*	0.0	—	—	—	
Lygaeidae								
Geocoris bullatus	Pea aphids	Sunflower seed	—	20.0	100.0^a	—	—	Tamaki and Weeks 1972
	Pea aphids	Sunflower seed, green bean	—	80.0	100.0^a	—	—	
Geocoris pallens	Pea aphids	Sunflower seed	—	8.0	0.0	—	—	

Table 1. continued

	Pea aphids	Sunflower seed, green bean	—	82.0	100.0[a]		
Geocoris pallens	Looper eggs	Cotton nectar	−1.6	7.2	—	—	−1.9[b]	DeLima and Leigh 1984[c]
Geocoris punctipes	Tubermoth eggs	Green bean	5.0	-6.7	111.2*	1.9	4.4[b]	Dunbar and Bacon 1972
	Pea aphids	Green bean	—	52.0*	100.0[a]	100.0[a]	—	
Geocoris punctipes	*Heliothis* eggs	Green bean	−15.3	2.5	−6.5	—	−8.4[b]	Cohen and DeBolt 1983
	Lygus eggs	Green bean	−2.5	4.0	22.2	—	0.7[b]	
Geocoris punctipes	*Spodoptera* eggs	Green bean	−2.3	0.0	−12.7	—	−8.7	Naranjo and Stimac 1985
	Spodoptera eggs	Soybean leaf	−0.9	26.7*	−9.8	—	2.2	
	Spodoptera eggs	*Chenopodium* leaf	−0.5	33.4*	−1.4	—	8.8	
Miridae								
Campylomma livida	*Heliothis* eggs	Cotton tips, squares	−15.8*	28.5*	288.9*	48.6*	—	Chinajariyawong and Walter 1990[d]
Deraecoris signatus	Cotton aphids	Cotton tips, squares	−4.6*	10.0	68.5	13.3	—	Chinajariyawong and Harris 1987[d]
Lygus hesperus	*Spodoptera* larvae	Green bean	0.0	27.8*	—	—	—	Bryan et al. 1976[e]
	Spodoptera larvae	Lettuce	23.1*	14.4*	—	—	—	

Table 1. continued

Pentatomidae								
Podisus maculiventris	*Leptinotarsa* larvae	Potato leaf	−10.0 *	27.5	—	—	−6.6	Ruberson et al. 1986

Values are reported as percentage increases with supplemental plant food over prey alone. Asterisks denote statistically significant differences ($P < 0.05$) with supplemental plant feeding as reported by the cited authors. Most authors did not report statistical analyses of nymphal survival rates. Negative percentages indicate a decline in the specified life history trait with supplemental plant feeding. Percentage change in nymphal survival calculated as the difference between percentage survival values.

[a] Denotes that nymphs or adults or both unable to complete development or reproduce on prey alone.

[b] Female and male weight.

[c] Data averaged over 3 different nectaried cottons.

[d] Data averaged over separate studies of cotton tips and cotton squares as plant supplements.

[e] Data from 25°C studies.

potential for problems in future studies and exercise care in interpreting the results of past studies.

Supplemental Prey Feeding. The consistent importance of supplemental feeding on prey leaves little doubt that carnivory is the main feeding niche of the species that have been examined (Table 2). *O. insidiosus* and *O. tristicolor* may be unique among predaceous Heteroptera in their ability to complete nymphal development on plant diets alone. Regardless, the addition of thrips, mites, or *H. virescens* eggs to diets of green bean or pollen reduced developmental times by 22–29%, and in some instances nymphal survival was greatly improved (Table 2). Again, prey quality was important, but more so for adults than nymphs. For example, fecundity increased 168% in *O. insidiosus* that were fed supplemental *H. virescens* eggs in comparison with predators given only pollen, but fecundity and longevity were reduced when pollen alone was supplemented with thrips. The mirids *L. hesperus* and *Spanogonicus albofasciatus* (Reuter) can complete development and reproduce, respectively, on diets of plants alone, but supplemental feeding on prey significantly enhances these life history traits. The ability of these insects to use plant food is not surprising, especially for *L. hesperus*, which is considered a serious pest of alfalfa and cotton. Within the remaining families studied, prey-feeding was essential for nymphal maturation and it greatly increased the longevity and fecundity of adults.

Plant Feeding Alone. The extent to which plant food can be used as the sole source of nutrients varies taxonomically (Table 3). As already noted, anthocorids can complete nymphal development and reproduce on plant foods alone. *O. insidiosus* completed development on *Acer* spp. pollen and was able to reproduce at a rate not much lower than individuals provided prey (see Table 2; Kiman and Yeargan 1985). *O. insidiosus* also can complete nymphal development on pollen of common mullein (McCaffrey and Horsburgh 1986), and Fauvel (1974) noted the same for *Orius vicinus* Ribaut feeding on an unspecified pollen. Several predaceous lygaeids, mirids, and pentatomids can develop through several stadia on certain plant foods, and some predatory pentatomids require no food as 1st instars (e.g., Mukerji and LeRoux 1965, Waddill and Shepard 1974, DeClercq and Degheele 1990). Conversely, even though some species of nabids and reduviids can extract moisture and useful nutrients from certain plants, their ability to do so is relatively limited. For example, 1st-instar nymphs of *Nabis* spp. feeding on dandelion pollen, sunflower seeds, or green beans survived from 60 to 650% longer than if given only water, but no development occurred.

Quality of the plant food also significantly influences the extent to which phytophagy can be used to support development or survival or both. For example, *G. pallens* can develop to the 5th stadium and adult survival is increased nearly 4 times on cotton nectar; however, cotton leaf sap does not support development past the 1st instar. Likewise, some *G. punctipes* developed to the 5th stadium on green bean or sunflower seed, but few developed

Table 2. Influence of supplementing various plant-only diets with prey food on selected life history traits of some predaceous heteropterans

Species	Plant food	Supplemental prey food	Nymph		Adult female		Reference
			Development time	Survival to adult	Fecundity	Longevity	
Anthocoridae							
Orius insidiosus	Pollen	Thrips	–22.2*	5.0	–3.0	–61.8*	Kiman and Yeargan 1985
	Pollen	*Heliothis* eggs	–28.6*	2.7	168.0*	11.9	
	Pollen	Mites	–27.5*	2.7	20.9	–28.5	
	Green bean	Thrips	^{a}	76.9*	—	—	
	Green bean	*Heliothis* eggs	^{a}	87.1*			
	Green bean	Mites	^{a}	75.0*	—	—	
Orius tristicolor	Green bean	Thrips	—	9.2*	128.6*	69.0^{b}	Stoltz and Stern 1978a^{c}
Orius tristicolor	Bean leaf	Mites	—	—	—	589.2	Askari and Stern 1972
Orius tristicolor	Green bean	Thrips	–28.0*	40.0	—	—	Salas-Aguilar and Ehler 1977
	Pollen	Thrips	–28.2*	27.5	—	—	
	Green bean, pollen	Thrips	—	—	137.5*	126.5*	
Lygaeidae							
Geocoris bullatus	Sugarbeet leaf	Green peach aphid	—	—	100.0^{d}	227.3^{b}*	Tamaki and Weeks 1972
	Sugarbeet leaf, sunflower seed	Green peach aphid	—	—	120.6	–13.6^{b}	

Table 2. continued

Geocoris pallens	Beet leaf	Leafhopper eggs	[a]	—	>80.0	>129.2[b]	York 1944
Geocoris pallens	Cotton leaf	Cotton aphid	—	—	—	150.0[b,e]	Ridgway and Jones 1968
Geocoris punctipes	Beet leaf	Leafhopper egg	—	—	—	> 63.5[b,f]	York 1944
Geocoris punctipes	Green bean	*Spodoptera* eggs	[a]	63.3*	105.3[g]*	—	Naranjo and Stimac 1985
	Soybean leaf	*Spodoptera* eggs	[a]	90.0*	102.5[g]*	—	
	Chenopodium leaf	*Spodoptera* eggs	[a]	96.7*	177.1[g]*	—	
Miridae							
Campylomma livida	Cotton tips, squares	*Heliothis* eggs	[a]	81.5*	100.0[d]	175.6*	Chinajariyawong and Walter 1990[h]
Deraecoris signatus	Cotton tips, squares	Cotton aphids	[a]	88.0*	100.0[d]	279.2*	Chinajariyawong and Harris 1987[h]
Lygus hesperus	Green bean	*Spodoptera* larvae	–27.8*	14.8*	—	—	Bryan et al. 1976[i]
	Lettuce	*Spodoptera* larvae	–23.8*	14.2*	—	—	
Spanogonicus albofasciatus	Green bean	Pea aphids	—	—	75.7*	–8.3	Musa and Butler 1967
	Green bean	*Heliothis* larvae	—	—	129.2*	17.6	
	Green bean	*Spodoptera* larvae	—	—	186.1*	44.1	
Nabidae							
Nabis americoferus	Cotton leaf	Cotton aphid	—	—	—	0.0[b,e]	Ridgway and Jones 1968

Table 2. continued

Pentatomidae							
Podisus maculiventris	Green bean	*Tenebrio* larvae	—	—	100.0[d]	115.5*	Wiedenmann and O'Neil 1990[j]

Values are reported as percentage increases with supplemental prey food over plant food alone. Asterisks denote statistically significant differences ($P < 0.05$) with supplemental prey feeding as reported by the cited authors. Some authors did not report statistical analyses of nymphal survival rates. Negative values indicate a decrease in the specified life history trait with supplemental prey food. Percentage change in nymphal survival calculated as the difference between percentage survival values.

[a] Unable to complete nymphal development on indicated plant diet alone.

[b] Female and male longevity or survival

[c] Data averaged over three prey densities. Adult longevity reported as percent survival after 7 d.

[d] Adults unable to reproduce on plant food alone.

[e] Based on LT_{50} values for survival.

[f] Based on percentage adult survival after 20 d.

[g] Adults were allowed to feed on prey until mature (5 d). Fecundity comparisons were based on eggs per female per day.

[h] Data averaged over separate studies of cotton tips and cotton squares as plant food.

[i] Data from 25°C studies only.

[j] Adult longevity on prey diets averaged over large and small *Tenebrio* larvae provided every day.

Table 3. Influence of supplementing water-only diets with various plant foods on selected life history traits of some predaceous heteropterans

Species	Plant food	Survival to indicated stadium					Nymphal longevity	Adult longevity	Reference
		2	3	4	5	Adult			
Anthocoridae									
Orius insidiosus	Pollen	—	—	—	—	91.2	530.0*	—	Kiman and Yeargan 1985[a]
Lygaeidae									
Geocoris spp.	Beet leaf	—	—	—	—	—	—	-10.6	York 1944
Geocoris pallens	Cotton leaf	—	—	—	—	—	—	0.0	Ridgway and Jones 1968[b]
Geocoris pallens	Cotton nectar	77.0	74.6	48.2	12.7	0.0	—	381.8*	DeLima and Leigh 1984[c]
Geocoris punctipes	Pollen	0.0	—	—	—	—	251.4*	—	Stoner 1970
	Sunflower seed	57.1	33.9	9.8	0.9	0.0	357.1*	—	
	Green bean	28.3	10.9	2.2	2.2	2.2	268.6*	—	
	Cotton leaf	0.0	—	—	—	—	162.9*	—	
Geocoris punctipes	Green bean	50.0	10.0	3.3	0.0	—	207.5*	271.7*	Naranjo and Stimac 1985[d]
	Soybean leaf	6.7	0.0	—	—	—	12.5	6.7	
	Chenopodium leaf	16.7	0.0	—	—	—	27.5*	-10.0	

Table 3. continued

Miridae									
Campylomma livida	Cotton tips, squares	—	—	—	—	—	66.7*	75.0*	Chinajariyawong and Walter 1990[e]
Deraeocoris signatus	Cotton tips, squares	—	—	—	—	—	54.3*	4.5	Chinajariyawong and Harris 1987[e]
Nabidae									
Nabis americoferus	Cotton leaf	—	—	—	—	—	—	50.0	Ridgway and Jones 1968[b]
	Pollen	0.0	—	—	—	—	647.6*	—	Stoner 1972
	Sunflower seed	0.0	—	—	—	—	276.2*	—	
	Green bean	0.0	—	—	—	—	204.8*	—	
	Cotton leaf	0.0	—	—	—	—	0.0	—	
Nabis alternatus	Pollen	0.0	—	—	—	—	568.8*	—	
	Sunflower seed	0.0	—	—	—	—	500.0*	—	
	Green bean	0.0	—	—	—	—	287.5*	—	
	Cotton leaf	0.0	—	—	—	—	-31.3	—	
Nabis capsiformis	Pollen	0.0	—	—	—	—	473.7*	—	
	Sunflower seed	0.0	—	—	—	—	294.7*	—	
	Green bean	0.0	—	—	—	—	63.2*	—	
	Cotton leaf	0.0	—	—	—	—	5.3	—	
Pentatomidae									
Podisus acutissimus	Sunflower seed	100.0[f]	26.0	18.0	2.0	0.0	342.9*	—	Stoner et al. 1974
	Pollen	100.0	—	—	—	—	419.0*	—	
	Green bean	100.0	—	—	—	—	116.7*	—	
	Cotton leaf	100.0	—	—	—	—	76.2*	—	
Podisus maculiventris	Potato leaf	100.0[f]	—	—	—	—	6.1	—	Ruberson et al. 1986

Table 3. continued

Reduviidae									
Sinea complexa	Pollen	0.0	—	—	—	—	418.8*	—	Stoner et al. 1975
Sinea confusa	Pollen	0.0	—	—	—	—	478.8*	—	
	Sunflower seed	0.0	—	—	—	—	27.3	—	
	Green bean	0.0	—	—	—	—	33.3	—	
	Cotton leaf	0.0	—	—	—	—	6.1	—	
Zelus renardii	Pollen	0.0	—	—	—	—	509.4*	—	
	Sunflower seed	0.0	—	—	—	—	21.9	—	
	Green bean	0.0	—	—	—	—	18.8	—	
	Cotton leaf	0.0	—	—	—	—	-3.1	—	
Zelus socius	Pollen	0.0	—	—	—	—	794.3*	—	
	Sunflower seed	0.0	—	—	—	—	37.1	—	
	Green bean	0.0	—	—	—	—	34.3	—	
	Cotton leaf	0.0	—	—	—	—	-5.7	—	

Values are reported as percentage increases with the addition of plant food. Asterisks denote statistically significant differences ($P < 0.05$) with supplemental plant feeding as reported by the cited authors. Negative values indicate a decrease in the specified life history trait with supplemental plant food.

[a] Only total nymphal survival reported.

[b] Based on LT_{50} values for survival.

[c] Cotton leaves (not water) provided as the control diet. Data averaged over 3 nectaried cottons.

[d] Adult fecundity and longevity values derived from adults reared on prey and plant diets as nymphs, but provided only plant or water diets from eclosion.

[e] Data averaged over separate studies of cotton tips and cotton squares as plant food.

[f] *Podisus* spp. nymphs can complete the 1st nymphal stadia without food.

to even the 2nd stadium when fed soybean or *C. ambrosioides* leaves, and no development occurred on cotton leaves. Cotton leaf sap also was of little or no nutritive value to nabids and reduviids, although pollen, sunflower seeds, or green bean may support life for weeks (Table 3).

We cannot generalize about the ability of predaceous heteropterans to subsist as herbivores. For instance, the ability to complete development on plant food alone highlights the potential importance of phytophagy; however, the inability to develop on only 1 type of plant may not fully describe the extent to which a predator can utilize phytophagy during its life cycle. Some predators may need a combination of plant species or plant components (nectar, pollen, seeds), to obtain the essential nutrients for growth, development, or even reproduction.

Plant Feeding Versus Prey Feeding. So far we have been able to evaluate the relative value of prey or plant food as supplements to one another or to gauge the ability of predators to use plant food alone. Several of the studies examined also allowed for comparison of predator performance on plant-only versus prey-only diets (Table 4). Nymphs of *O. insidiosus* feeding on pollen take from 1.3 to 1.4 times longer to reach adulthood but have better or equal survivorship compared with those feeding on thrips, mites, or eggs of *H. virescens*. Similarly, nymphs of *O. tristicolor* take 1.2–1.5 times longer to complete development on green bean or pollen compared with thrips, but survivorship is higher when feeding on prey. Two percent of the *G. punctipes* nymphs tested reached adulthood on green bean or barley seed, but these individuals took up to 2.2 times longer to mature than did predators given prey. *L. hesperus* is the only other species examined in which both prey-only and plant-only diets permitted complete nymphal development. Even in this "herbivore," prey diets allowed faster development.

A Simple Simulation Study. To this point we have demonstrated the importance of phytophagy on single life history traits. The overall effect of plant-feeding on the population ecology of a species is more difficult to appreciate, particularly if the contributions of plant food appear relatively minor. Naranjo and Stimac (1985) studied the influence of supplemental plant sap feeding in *G. punctipes* preying on eggs of the fall armyworm. They concluded that plant food contributed only subtly by increasing developmental and survival rates in nymphs. They further suggested that such minor changes could alter the population age-structure and might influence the predator's effect on its prey.

We constructed a simple simulation model to test this hypothesis using published and unpublished data from Naranjo and Stimac's (1985) study. We used normal random number generators (Shannon 1975) to stochastically alter stadia-specific developmental times and age–specific oviposition rates based on observed means and standard deviations for these traits. Oviposition rates were estimated as the number of viable female eggs (1:1

Table 4. Comparison of prey-only with plant-only diets on selected life history traits of some predaceous heteropterans

Species	Prey food	Plant food	Nymph		Adult		Reference
			Development time	Survival to adult[a]	Fecundity	Longevity	
Anthocoridae							
Orius insidiosus	Thrips	Pollen	1.0:1.3*	68.0:91.2	—	—	Kiman and Yeargan 1985[b]
	Heliothis eggs	Pollen	1.0:1.4*	94.1:91.2	—	—	
	Mites	Pollen	1.0:1.4*	96.9:91.2	—	—	
Orius tristicolor	Thrips	Green bean	1.0:1.5*	90.0:42.5	—	—	Salas-Aguilar and Ehler 1977
	Thrips	Pollen	1.0:1.2 *	90.0:62.5	—	—	
Lygaeidae							
Geocoris bullatus	Pea aphids	Sunflower seeds	1.0:0.5[c]	0.0:0.0	—	—	Tamaki and Weeks 1972
Geocoris pallens	Pea aphids	Sunflower seeds	1.0:0.8[c]	0.0:0.0	—	—	
Geocoris punctipes	*Spodoptera* larvae	Green bean	1.0:2.2	100.0:2.2	—	—	Stoner 1970
	Spodoptera larvae	Barley seed	1.0:1.2	100.0:2.2	—	—	
	Spodoptera larvae	Sunflower seed	—	100.0:0.0	1.0:0.2*	1.0:0.9	

Table 4. continued

Miridae							
Campylomma livida	*Heliothis* eggs	Cotton tips, squares	—	53.0:0.0*	0.9:0.0[d]*	1.0:0.6*	Chinajariyawong and Walter 1990
Deraeocoris signatus	Cotton aphids	Cotton tips, squares	—	78.0:0.0*	20.2:0.0[d]*	1.0:0.3*	Chinajariyawong and Harris 1987
Lygus hesperus	*Spodoptera* larvae	Green bean	1.0:1.4 *	19.0:32.0*	—	—	Bryan et al. 1976[e]
	Spodoptera larvae	Lettuce	1.0:1.6 *	19.0:19.2	—	—	

Values are reported as the ratio of prey-feeding to plant-feeding. Asterisks denote statistically significant differences ($P < 0.05$) between diets as reported by the cited authors.

[a] Reported as actual percentage survival to adulthood.

[b] Nymphal development and survival were evaluated on green bean alone, but nymphs failed to mature.

[c] Nymphs failed to mature on prey or plant diets; ratio compares nymphal longevity.

[d] Ratios report actual fecundity because there was no reproduction on plant diets.

[e] Data from 25°C studies only.

sex ratio) laid each day. We used binomial random number generators (Shannon 1975) to simulate stadia- and age-specific survival rates for nymphs and adults, based on observed survival probabilities. Finally, the data of Crocker at al. (1975) were used to estimate daily stage-specific predation rates. The proportion of prey consumed (per day) by each nymphal instar and adult females was averaged across temperature, and predation rates were then normalized such that 1st instars consumed 1 prey item each day. The relative number of prey consumed each day was estimated to be 1, 1.88, 3.38, 4.73, 6.92, and 8.01 for 1st through 5th instars and adults, respectively. We ran 500 simulations for each of the 12 different plant diets and the control of supplemental water. Simulations were terminated when adults reached 15 d of age, and model output was summarized by calculating means and standard deviations for the total number of prey consumed and the number of female progeny produced per female. This latter statistic estimates the net reproductive rate based on oviposition during the 1st 15 d of adult life.

The overall effect of plant food on reproduction and predation was dramatic even though Naranjo and Stimac (1985) reported only minor changes in nymphal development and survival, and no statistically significant changes in reproduction (Fig. 1). Net reproductive rates on *Chenopodium ambrosioides* L. and *Ambrosia artemisiifolia* L. leaf sap increased by 50% over the control diet and by as much as 88% over a diet of *Crotalaria spectabilis* Roth. The rate of predation increased 40%, with a mean of 135 prey consumed on the control diet and a mean of 190 prey consumed with a supplemental diet of *C. ambrosioides* leaves. The low correlation between reproduction and predation resulted from the differing influence of particular plant diets on overall life history. For instance, prey consumption rates were not influenced by adult survival rates, which were >90% on all diets (S.E.N., unpublished data), but they were affected by nymphal survivorship which varied considerably with the type of plant food. Net reproductive rates were influenced by nymphal survival, but also were affected by subtle changes in age-specific schedules of oviposition not reflected in the summary statistics reported by Naranjo and Stimac (1985). Based on simplified assumptions of feeding behavior under ideal circumstances, this analysis suggests that what we perceive as minor changes in particular life history traits may have profound consequences on population growth and predation efficiency.

Indirect Evidence of Plant-Feeding Benefits

Nectaried Versus Nectariless Cottons. Extrafloral nectaries play an important role in the interactions between plants, herbivores, and their natural enemies (Bentley 1977, Rogers 1985). The nectariless trait in cotton is considered to be important in conferring resistance against several impor-

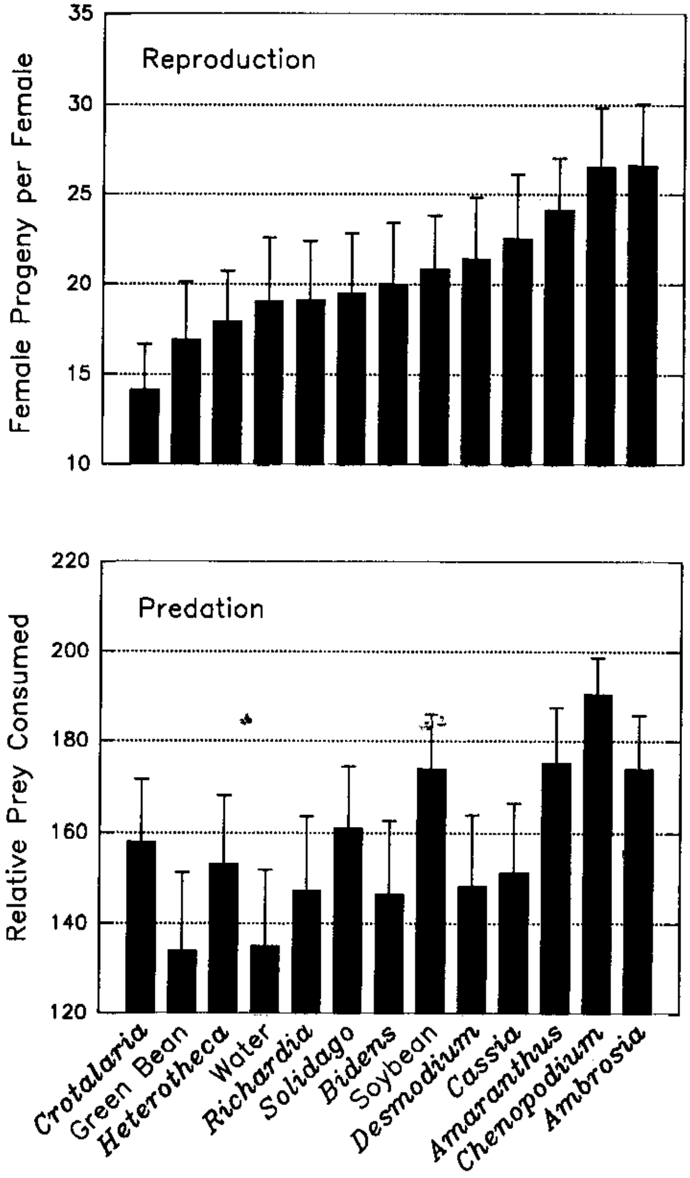

Fig. 1. Results of stochastic simulations of development, reproduction, and predation by *Geocoris punctipes* feeding on *Spodoptera frugiperda* eggs and the leaves of various plants. Error bars are ±SD. Female progeny per female approximates the net reproductive rate, and relative prey consumed estimates the number of prey consumed per individual from egg hatch until adults are 15 d old. Consumption rates were normalized so that 1st-instar nymphs consumed 1 prey per day.

tant pest species, but it also has been implicated in the reduction of populations of natural enemies (Bergman and Tingey 1979, Schuster and Calderon 1986). Comparative studies of cottons with and without extrafloral nectaries have provided an indirect means for estimating the importance of plant-feeding (by implication nectar-feeding) for various predatory insects (Hagen 1986). A number of studies have shown reductions in the densities of predaceous heteropterans in nectariless relative to nectaried cottons (Table 5). Statistically significant reductions were noted in 3 of 11 cases for *Orius* spp., 5 of 11 cases for *Geocoris* spp., 3 of 17 cases for *Nabis* spp, and 2 of 3 cases for 2 species of mirids. If we look just at numerical patterns, ignoring statistical significance and considering only those cases in which densities were reported, there were reductions of populations in nectariless cottons in 80% of the cases for *Orius* spp., all the cases for *Geocoris* spp., and 78% of the cases for *Nabis* spp. Overall, these results suggest that nectar-feeding may be relatively important to all these predator groups.

However, assessing the importance of phytophagy for predators from these types of studies is problematic. First, there are also significant reductions in potential prey species in nectariless cottons, particularly Lepidoptera (Lukefahr and Rhyne 1960, Lukefahr et al. 1965, Benschoter and Leal 1974, Wilson and Wilson 1976, Adjei-Maafo and Wilson 1983) and pest Heteroptera (Tingey et al. 1975, Schuster et al. 1976, Henneberry et al. 1977, Adjei-Maafo and Wilson 1983). In general, reductions in predator densities have been shown to be equal to or greater than reductions in pest densities (Schuster and Calderon 1986); however, it remains difficult to establish whether it is the absence of prey, nectaries, or both that causes reductions of predator population in nectariless cottons. Another concern is that the presence of nectaries does not ensure that nectar will be available to foraging predators. Nectar quantity varies on a daily and seasonal basis (Butler et al. 1972, Yokoyama 1978). In addition, other insects, such as ants, may remove significant quantities of nectar or even the nectary itself (Agnew et al. 1982). Also, there may be differences between the cultivars beyond the presence or absence of nectaries. For instance, Rogers and Sullivan (1986) found differences in developmental and survival rates of nymphal *G. punctipes* reared on resistant and susceptible soybean foliage.

Plot size is another factor that may contribute to problems with interpretation. Because predators are mobile, small plots allow free movement between nectaried and nectariless plots and thus, small plots may largely measure preference. In support of this, Adjei-Maafo and Wilson (1983) showed that reductions in insect populations in nectariless cotton declined with increasing plot size and suggested that the effect of the nectariless trait may be insignificant in commercial–size fields. However, based on plots ranging from 0.001 to 42 ha in size (Table 5), there is no clear trend in predator population reductions between large and small plots. Large-plot

Table 5. Reductions in populations of various predaceous heteropterans in nectariless cotton in comparison with nectaried cotton

Species	% reduction	Plot size, ha	Reference
Anthocoridae			
Orius insidiosus	22*	1	Schuster et al. 1976
	43*	3	
	18	14–42	
	0	0.001	Agnew et al. 1982
	21	0.001	
Orius tristicolor	–15	1	Flint et al. 1991
	–5	8	Henneberry et al. 1977
	11	8	
	6	0.005	
	18	0.005	
Orius spp.	52*	0.1–4	Adjei-Maafo and Wilson 1983
Lygaeidae			
Geocoris lubra	41*	0.1–4	Adjei-Maafo and Wilson 1983
Geocoris punctipes	0	3	Schuster et al. 1976
	0	14–42	
	0	0.001	Agnew et al. 1982
	88*	0.001	
Geocoris uliginosus	0	14–42	Schuster et al. 1976
Geocoris spp.[a]	6	8	Henneberry et al. 1977
	42*	8	
	23*	0.005	
	31*	0.005	
	5	1	Flint et al. 1991
Miridae			
Deraecoris signatus	51*	0.1–4	Adjei-Maafo and Wilson 1983
Spanogonicus albofasciatus	–21	3	Schuster et al. 1976
	79*	14–42	
Nabidae			
Nabis alternatus	0	3	Schuster et al. 1976
	0	14–42	
Nabis deceptivus	0	14–42	
Nabis capsiformis	0	3	
	0	14–42	
	53*	0.1–4	Adjei-Maafo and Wilson 1983
Nabis roseipennis	0	3	Schuster et al. 1976
	0	14–42	
Nabis spp.	41*	1	

Table 5. continued

5	3	
88	14–42	
0	8	Henneberry et al. 1977
29	8	
–25	0.005	
34*	0.005	
–5	1	Flint et al. 1991
45	0.2	Flint et al. 1986

Asterisks denote that a statistically significant reduction was reported ($P < 0.05$). Reductions of 0% indicate that numerical data were not presented, but authors indicated no significant differences in comparing predator densities in nectaried with nectariless cottons. Negative values indicate an increase in nectariless cotton.

[a] Probably *G. punctipes* and *G. pallens*

studies probably minimize migrational effects and mainly estimate reproductive effects caused by changes in the availability of nutritional resources. Both preference and reproduction are potentially meaningful in evaluating the importance of nectar-feeding by predators. Preference for nectaried cotton may suggest that predators actively seek nectar, whereas reductions in population growth in nectariless cotton may suggest that extrafloral nectar is an important diet component. We hypothesize that behavioral preferences and lower reproductive rates both contribute to reductions of predator populations in commercial-size fields of nectariless cotton.

There is little direct evidence to test this hypothesis, but predaceous heteropterans are known to feed on and benefit from cotton nectar. Extrafloral cotton nectar is rich in sugars (Butler et al. 1972) and contains a number of amino acids, many of which are essential for insect growth and development (Hagen 1986). In the absence of prey, immature and adult *G. pallens* lived longer when individuals were confined on a cotton leaf with a nectary in comparison with one without a nectary (DeLima and Leigh 1984). Yokoyama (1978) observed *G. pallens* and *O. tristicolor* feeding on extrafloral nectaries in cotton and suggested that nectar probably was an important food resource only when prey were scarce. Yokoyama's observation is supported by studies showing that nectar feeding in *G. punctipes* is reduced when prey are available (Thead et al. 1985, Schuster and Calderon 1986). Elucidating the role of cotton nectar-feeding on the biology and population dynamics of predatory Heteroptera will require controlled studies on a broader range of species.

Plant Association Studies. The abundance of predators also may be influenced by the presence or absence of certain weeds or ground covers that may supply pollen, floral and/or extrafloral nectar, seeds, and plant sap. For example, Bugg et al. (1987) examined the effect of knotweed, *Polygonum aviculare* L., on populations of various predators. *Geocoris* spp. were frequently found feeding on knotweed flowers, and adult *G. punctipes* lived longer when housed in cages with knotweed than when housed with alfalfa. These authors also found higher densities of *Geocoris* spp. on the ground in plots of pepper plants plus knotweed than in plots without knotweed. Conversely, they found that the presence of knotweed had no significant effect on *Orius* sp. densities on pepper plants in the same plots. Bugg et al. (1990), investigating predator densities in various winter cover crops in Georgia, found significant differences in the number of *Geocoris* spp. Densities were highest in the vetches, lentil, subterranean clover and crimson clovers during March and April, and extremely high densities of *Geocoris* spp. were found on lentil, arrowleaf clover, and berseem clover in June. No *Geocoris* spp. were found in ryegrass or rye plots during the same period. Densities of *O. insidiosus* also were significantly greater in narrow-leafed lupine, the vetches and lentil, but none was found in rye or canola. In a related study, Bugg et al. (1991) examined the abundance of *G. punctipes* in a number of cover crops intercropped with cantaloupe. They found that *G. punctipes* were more abundant in subterranean clover than in other cover crops, and suggested that the higher numbers were responsible for increased predation on fall armyworm egg masses placed on cantaloupe.

It is difficult to separate the influences of prey abundance from the availability of important plant resources provided by associated plants. By themselves, the numerous studies of plant associations (see reviews by Cromartie 1981, Sheehan 1986) do not directly improve our knowledge of the role of plant feeding in predaceous species. However, based on the importance of plant feeding demonstrated in the laboratory, this facet of the tritrophic interaction deserves greater attention in field studies. Determining the underlying causes of the correlations between certain plants and densities of predators might be aided by a better understanding of how and when predators utilize plant resources in nature.

Observational Studies of Plant Feeding. Plant feeding by predaceous heteropterans has been frequently observed in nature, and some accounts suggest that phytophagy may serve not only as a strategy for surviving periods of prey scarcity but as a means of providing complementary food resources. The most complete work published to date of predator feeding behavior in the field is that of Crocker and Whitcomb (1980), who studied three species of *Geocoris*. They observed *G. punctipes*, *G. bullatus*, and *G. uliginosus* (Say) collectively feeding on 8 diverse families of herbaceous angiosperms in northern and central Florida. They observed *Geocoris* spp. feeding on all above-ground structures, including leaves, stems, flowers, and seeds. Although many lygaeids are seed feeders, Crocker and Whitcomb's evidence indicated no preference for seeds or any other particular plant part. Also, there was no apparent correlation of plant feeding with environmental characteristics. They observed *Geocoris* feeding on plants from April to November, from 20 to 34°C, and under a wide range of humidities. Finally, they reported that potential prey almost always were present when plant feeding was observed. In another field study, Burgess et al. (1983) observed *G. bullatus* feeding on the green pods of *Brassica juncea* L.

References to plant feeding by anthocorids also are common in the literature (e.g., references cited in Lattin et al. 1989). *O. insidiosus* adults are attracted to corn silks (Reid and Lampman 1989, Reid 1991), and feed on corn pollen in the field (Dicke and Jarvis 1962, Coll and Bottrell 1991). Whether or not this behavior is important is somewhat controversial. Dicke and Jarvis (1962) suggested that *O. insidiosus* adults feed on pollen rather than prey during silking, whereas Reid (1991) proposed that attraction to silks makes this species a valuable biological control agent of corn earworm eggs laid on silks.

The importance of plant feeding in nabids also has been questioned. Taylor (1949) reported that nymphs of *Nabis alternatus* Parshley were not able to complete development on alfalfa, and argued that supplemental plant sap was unnecessary for development. Lattin (1989) stated that some plant feeding may occur in nabids, but suggested that obtaining moisture is the chief objective. Ridgway et al. (1967) reported high mortality of *N. americoferus* Carayon caged on systemically treated cotton plants, and Ridgway and Jones (1968) concluded that this species will feed on cotton leaf sap even in the presence of potential prey. Burgess et al. (1983) collected *N. alternatus* and *N. subcoleoptratus* (Kirby) adults from green *B. juncea* pods, and found *N. alternatus* carried the yeast *Nematospora coryli* Peglion, an economically important disease of mustard. Lattin (1989) suggested that the insects had obtained the yeast by feeding on infected prey, but Burgess et al. (1983) noted that the nabids fed directly on the pods.

Balduf (1939) observed female *Phymata* sp. with their mouthparts in flowers and suggested they may feed on nectar in times of prey scarcity. When reared in the laboratory on *Drosophila*, he observed 1st-instar phymatids feeding on banana peels that he had supplied to the prey (Balduf 1941). Miller (1971) also noted that members of the Phymatidae feed on nectar or plant sap when prey are absent.

Podisus maculiventris (Say) also feeds on plants in nature. Chandler (1950) reported a feeding injury known as "catfacing" on peaches when various stink bugs were caged on peach trees without prey. Morris (1963) found that *P. maculiventris* routinely fed on apple leaves in the presence of abundant prey, *Hyphantria cunea* Drury, with individual plant-feeding episodes lasting up to 3 h. This plant feeding was more frequent when adults were >20 d old. Wiedenmann and O'Neil (1991) observed that *P. maculiventris* spend considerable time feeding on seedling bean plants, and they noticed no differences in this behavior attributable to prey density. McPherson (1982) cited references of observations of plant feeding in 7 species of stink bugs in the subfamily Asopinae. He also cites references indicating predation in ≥14 species of phytophagous stink bugs but largely discounted these reports.

Mirids are a difficult group to categorize because many are both phytophagous and carnivorous (Miller 1971). For example, McMullen and Jong (1970) observed that *Campylomma verbasci* (Meyer), a mirid pest of apple in Ontario and Nova Scotia, is also a predator of pear psylla, *Psylla pyricola* Förster. Thistlewood et al. (1990) observed that this mirid preferred mullein inflorescences and suggested this may be caused by the higher concentration of plant nutrients. Despite its pest status, this insect apparently requires prey for the completion of development (McMullen and Jong 1970). The importance to *C. verbasci* of phytophagy and predation are discussed by Thistlewood and Smith (this volume).

Conclusions

Predaceous heteropterans, like many other generalist predators, display considerable plasticity in the types of prey and plant foods that they utilize in nature. Closer scrutiny of this omnivorous habit would probably reveal that many predators have adopted feeding strategies that optimize the mix of essential nutritional components (León and Tumpson 1975, Greenstone 1979, Rapport 1980). Some early literature variously described the importance of phytophagy in this group. For example, York (1944) concluded that plant feeding was only a means of obtaining essential moisture for several *Geocoris* species. Conversely, Sweet (1960) suggested that carnivory may not be "obligatory" in some *Geocoris* spp. because these insects were able to survive for extended periods on sunflower seeds. To what extent then do plants contribute to the overall nutritional requirements of predaceous heteropterans? It may be instructive to view this question from the perspective of optimal foraging by predators. In optimal foraging parlance, perfectly complementary resources are those that satisfy essential needs and must be taken together in the diet. At the other extreme, perfectly substitutable resources are ones that satisfy the same essential need. Finally, imperfectly substitutable resources are those that may be sufficient alone but improve fitness if taken together.

The answer to our question clearly depends on the quality of the prey and plant foods, and the developmental stage of the predator. Kiman and Yeargan's (1985) study of *O. insidiosus* feeding on maple pollen provides the only evidence that phytophagy may be perfectly substituted for carnivory throughout the predator's entire life cycle. Some mirids also may perfectly substitute phytophagy for carnivory (e.g., *L. hesperus* and *S. albofasciatus*), but their status as "predators" is questionable. For these species it may be more appropriate to suggest that carnivory can be substituted for phytophagy. Phytophagy may be substitutable for carnivory in several species during certain developmental stages. Stoner (1970) demonstrated that *G. punctipes* could complete development on barley seeds or green beans, and he also showed that *G. punctipes* could reproduce on sunflower seeds alone if the immatures were reared to adulthood on prey diets. Likewise, Tamaki and Weeks (1972) demonstrated that *G. bullatus* could reproduce on sunflower seeds and sugarbeet leaves, but the adults used in their study were collected in the field where they most likely had fed on prey. Finally, Stoltz and Stern (1978a) found that field-collected adults of *O. tristicolor* were able to reproduce on green bean alone, but these, too, likely fed on prey before the predators were captured. All of these partial life-stage studies probably represent imperfect substitutability, because the addition of prey would significantly increase rates of development, survival, and reproduction.

The importance of phytophagy is probably best gauged as a complement to prey feeding because most predaceous heteropterans regularly feed on a mixture of prey and plant foods in nature. Supplemental phytophagy has been shown to be essential for reproduction of *G. bullatus* and *G. punctipes* feeding on pea aphids (Dunbar and Bacon 1972, Tamaki and Weeks 1972), but plant feeding did not significantly increase reproductive rates in *G. punctipes* feeding on lepidopteran eggs (Cohen and DeBolt 1983, Naranjo and Stimac 1985). In the latter case, plant feeding provides essential moisture, but sufficient water could be obtained from an exophytic source. Likewise, higher quality prey species could be substituted for plant material to supplement a diet of pea aphids. In many of the studies examined (Tables 1 and 2), supplemental plant food significantly enhanced various life history traits, but phytophagy cannot strictly be considered complementary in many cases because development and reproduction are possible without plant food. We cannot easily extrapolate findings based on diets of single prey or plants (or both) to the diversity of dietary components likely to be used by predators, even in simple agroecosystems. Thus, based on extant laboratory studies, we cannot adequately assess or categorize the value of phytophagy.

However, several lines of recent research lead us to suggest that phytophagy plays a central role in the life history and population ecology of predaceous Heteroptera. First, Cohen (1990, this volume) has found that several predaceous heteropterans produce amylases that may function to break down plant materials. Moreover, these enzymes are found not only in *G. punctipes* and *P. maculiventris*, members of predominantly phytophagous families, but also in nabids and reduviids. Thus, many predaceous Heteroptera may be physiologically equipped for plant feeding and it seems likely that such an adaptation occurred because of some selective advantage. Secondly, O'Neil and Wiedenmann (1987), Wiedenmann and O'Neil (1990), and Wiedenmann et al. (this volume), have found that a generalist predator, *P. maculiventris*, may rely on phytophagy to sustain life between prey meals, meals that in some agricultural systems may be infrequent. Prey scarcity may be a problem common to many generalist predators that inhabit disturbed, short-durational agricultural systems. Moreover, evidence from laboratory studies suggests that the most abundant predator species in many agricultural systems can utilize certain plant foods alone to extend survival for considerable periods. The need to bridge gaps in prey availability may be universal in annual crops, and adaptations that permit the utilization of plant food may be key to the existence of many, if not all, predaceous heteropterans.

Areas for Future Research

More comprehensive studies in the laboratory and field would greatly enhance our understanding of how predators function in natural and agricultural systems. Most of the work on phytophagy in predaceous Heteroptera is preliminary, and many lines of research are suggested. At the proximate level, more work needs to be done on exactly what nutritional benefits, if any, heteropteran predators are deriving from plant-feeding. Moisture is essential, but plant feeding also may be critical for attaining essential carbohydrates and amino acids. These nutritional aspects are even more significant in light of the presence of enzymes in some species capable of breaking down plant materials. The functions of these physiological tools must be explored more fully. Symbionts or symbiont organs have not been reported in predaceous heteropterans (Slater and Carayon 1963). However, the presence of gut symbionts in plant-feeding predators should be investigated more thoroughly and their role in nutrition evaluated. The ramifications of host plant resistance on predator biology and ecology also should be more fully explored, particularly from a multitrophic perspective (Orr and Boethel 1986). Factors other than nutrition may be important as well. For instance, are the defensive and attractant compounds in the scent glands of Heteroptera derived from plants? Also, what is the relationship between plant feeding by predators and the probability of infection of the host plant by phytopathogens? Finally, further work is needed to define the effect of systemic insecticides on the population dynamics and prey control efficacy of predaceous heteropterans.

At the ultimate level, we need more careful life history studies that evaluate more realistic mixtures of different prey and plant foods. These studies need to be conducted in a comparative manner with a wider range of species within and among heteropteran groups that are largely predaceous or phytophagous. Life history studies need to be conducted so that important parameters, such as net reproductive rates, generation times, intrinsic rates of increase, and reproductive fitness can be estimated and compared. Such estimates are critical before broader ecological and evolutionary questions regarding phytophagy can be addressed. For instance, careful measures of reproductive fitness could be used to test optimal foraging theory that incorporates nutritional balance as a key element (León and Tumpson 1975, Rapport 1980). Life history studies would also contribute greatly to the growing body of knowledge and theory on tri-trophic interactions and also might help unravel the evolution of carnivory and phytophagy within the Heteroptera. These studies will depend on careful observation of natural feeding behaviors and an understanding of the ecological factors that determine when, if, and to what extent, phytophagy will occur.

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