

# Health food versus fast food: the effects of prey quality and mobility on prey selection by a generalist predator and indirect interactions among prey species

MICKY D. EUBANKS and ROBERT F. DENNO Department of Entomology, University of Maryland, College Park, U.S.A.

**Abstract.** 1. In order to understand the relative importance of prey quality and mobility in indirect interactions among alternative prey that are mediated by a shared natural enemy, the nutritional quality of two common prey for a generalist insect predator along with the predator's relative preference for these prey was determined.

2. Eggs of the corn earworm *Helicoverpa zea* (Lepidoptera: Noctuidae) were nutritionally superior to pea aphids *Acyrtosiphum pisum* (Homoptera: Aphididae) as prey for big-eyed bugs *Geocoris punctipes* (Heteroptera: Geocoridae). Big-eyed bugs survived four times as long when fed corn earworm eggs than when fed pea aphids. Furthermore, only big-eyed bugs fed corn earworm eggs completed development and reached adulthood.

3. In two separate choice experiments, however, big-eyed bugs consistently attacked the nutritionally inferior prey, pea aphids, more frequently than the nutritionally superior prey, corn earworm eggs.

4. Prey mobility, not prey nutritional quality, seems to be the most important criterion used by big-eyed bugs to select prey. Big-eyed bugs attacked mobile aphids preferentially when given a choice between mobile and immobilised aphids.

5. Prey behaviour also mediated indirect interactions between these two prey species. The presence of mobile pea aphids as alternative prey benefited corn earworms indirectly by reducing the consumption of corn earworm eggs by big-eyed bugs. The presence of immobilised pea aphids, however, did not benefit corn earworms indirectly because the consumption of corn earworm eggs by big-eyed bugs was not reduced when they were present.

6. These results suggest that the prey preferences of generalist insect predators mediate indirect interactions among prey species and ultimately affect the population dynamics of the predator and prey species. Understanding the prey preferences of generalist insect predators is essential to predict accurately the efficacy of these insects as biological control agents.

**Key words.** Apparent competition, indirect interactions, predator preferences, prey quality, prey selection.

## Introduction

An individual generalist insect predator attacks a diversity of prey species during its life (Crocker & Whitcomb, 1980; Mills, 1982; Loreau, 1983; Araya & Haws, 1988; Nagai, 1991).

Correspondence: Micky D. Eubanks, Department of Entomology and Plant Pathology, 301 Funchess Hall, Auburn University, AL 36849, U.S.A. E-mail: meubanks@acesag.auburn.edu

Despite the often impressive number of prey species consumed, predators do not necessarily detect or attack every insect they encounter (Crocker & Whitcomb, 1980; Ohgushi, 1988). Generalist predators often have discernible preferences for prey, frequently attacking certain insect species while avoiding others (Richards, 1982; Awan, 1985; van Straalen, 1985; Houck, 1986; Wyatt & Foster, 1989; Digweed, 1993). Although many generalist insect predators are relatively well studied because of their economic importance, surprisingly

little is known about the prey selection process of these animals. These data are essential to predict the efficacy of generalist predators as biological control agents and to understand the effects of alternative prey on complex direct and indirect interactions involving generalist predators and their prey species.

Prey selection by generalist insect predators could have important consequences for prey populations. The impact of a generalist predator on any given prey species will depend not only on the abundance and susceptibility of that prey species but also on the abundance and susceptibility of other species that share the same enemy (Holt & Lawton, 1994). For example, two prey species, A and B, live in the same habitat and share the same enemy, a generalist insect predator. If the generalist predator does not prefer either species, the indirect effects of species A on species B and species B on species A will depend solely on their abundance. An increase in species A will tend to relax predation on species B and vice versa. Thus, an increase in the density of species A would have an indirect, short-term, positive effect on species B (Holt, 1977; Holt & Lawton, 1994). If the generalist insect predator prefers one of the prey species to the other, the outcome of interactions between the prey species and their shared predator would be more difficult to predict. If the predator preferred species B, an increase in species A would not necessarily reduce predation on species B. Understanding the prey selection process of generalist insect predators not only allows ecologists to predict the impact of a predator on a single prey species but also allows ecologists to predict the impact of a generalist predator on multiple prey species and understand indirect interactions that occur among prey species that share the same enemy (Holt & Lawton, 1994).

Potential prey encountered by generalist insect predators often differ greatly in nutritional quality, mobility, size, colour, odour, and taste, and most predaceous insects use one or more of these characteristics in the prey selection process (Richards, 1982; Awan, 1985; van Straalen, 1985; Houck, 1986; Wyatt & Foster, 1989; Digweed, 1993; but see Loreau, 1983 for an example of a predator with rather indiscriminate tastes). Optimal foraging models based on the caloric and nutritive value of prey predict that nutritional quality relative to foraging costs should be the most important criterion used in prey selection (Stephens & Krebs, 1986; Bernays & Bright, 1991; Waldbauer & Friedman, 1991). There is, however, no consensus among studies of generalist insect predators that prey quality is the most important criterion used in prey selection. In laboratory choice tests, several species of insect predators (e.g. the carabid beetle *Agonum dorsale*) selected the most nutritious prey (i.e. the prey whose consumption resulted in enhanced survival, increased fecundity, etc.) (Heitmans *et al.*, 1986; Nagai, 1991; Bilde & Toft, 1994). Yet, almost as many studies of generalist insect predators have found that they do not consistently select the most nutritious prey (Siddique & Chapman, 1987; Hagler & Cohen, 1991; Hazzard & Ferro, 1991; de Clercq & Degheele, 1994). For example, many studies have shown that generalist insect predators fed lepidopteran or coleopteran eggs have higher survival, shorter development times, and are more fecund than

when fed other prey species (Cohen & Debolt, 1983; Siddique & Chapman, 1987; Kawooya *et al.*, 1988; de Clercq & Degheele, 1994; Izumi *et al.*, 1994). These same predators, however, often attack nutritionally inferior prey species when given a choice (Siddique & Chapman, 1987; Hagler & Cohen, 1991; Hazzard & Ferro, 1991; de Clercq & Degheele, 1994).

One important prey characteristic used by insect predators to select prey is prey mobility, however the effect of prey mobility on prey selection appears to be predator-specific. For example, assassin bugs appear to attack mobile prey species preferentially (Rosenheim & Wilhoit, 1993; Rosenheim *et al.*, 1993), while other predators appear to select immobile prey. Prey mobility has frequently been inferred as an important mechanism of prey selection but definitive studies are lacking for almost all taxa of generalist insect predators (Foglar *et al.*, 1990; Hagler & Cohen, 1991; Hazzard & Ferro, 1991) and no published study has manipulated prey mobility.

The goal of the study reported here was to determine the relative importance of quality and mobility in the prey-selection process of a generalist insect predator to gain insight into how prey behaviour mediates indirect interactions among prey that share the same predator. To accomplish this goal, a common heteropteran predator, the big-eyed bug *Geocoris punctipes* (Heteroptera: Geocoridae) and two of its prey species, eggs of the corn earworm *Helicoverpa zea* (Lepidoptera: Noctuidae) and pea aphids *Acyrtosiphum pisum* (Homoptera: Aphididae) were studied. A series of laboratory experiments was used to: (1) quantify the relative nutritional quality of the two prey species, (2) measure the prey preference of the predator, and (3) manipulate prey mobility to determine its role as a mechanism underlying prey selection.

## Study system

### *Predator*

Big-eyed bugs *Geocoris punctipes* (Heteroptera: Geocoridae) are omnivorous, generalist predators that attack a diverse range of prey species (Champlain & Scholdt, 1966; Lawrence & Watson, 1979; Crocker & Whitcomb, 1980; Cohen & Debolt, 1983; Eubanks & Denno, 1999a). Big-eyed bugs are known to attack Collembolla, Orthoptera, Homoptera, Heteroptera, Thysanoptera, Coleoptera, Diptera, and Lepidoptera (Radio & Sweet, 1982). Despite the diverse taxa consumed by these predators, big-eyed bugs often ignore potential prey species in the field and the mechanism of prey selection by big-eyed bugs is poorly understood (Crocker & Whitcomb, 1980; Eubanks & Denno, 1999a,b). Although many economically important predators such as big-eyed bugs are well studied and much is known about some components of their predatory behaviour [e.g. the effect of temperature on prey consumption by big-eyed bugs (Crocker *et al.*, 1975; Chow *et al.*, 1983)], few studies have investigated the effects of prey nutritional quality and mobility on prey selection by big-eyed bugs or other generalist insect predators.

### Prey

The prey selection process of big-eyed bugs was studied by quantifying the consumption of two very different prey species by big-eyed bugs. Eggs of the corn earworm *H. zea* are relatively small, completely sessile, and contain the developing moth embryo and its associated yolk. Corn earworm eggs contain high concentrations of nitrogen and are consequently considered high quality prey for many generalist insect predators (Cohen & Debolt, 1983; Kawooya *et al.*, 1988; Izumi *et al.*, 1994). By contrast, pea aphids *A. pisum* are relatively mobile and are considered relatively low quality prey for many generalist insect predators (Champlain & Scholdt, 1966; Cohen & Debolt, 1983).

## Methods

### Nutritional quality of prey

To quantify the relative nutritional quality of corn earworm eggs and pea aphids relative to big-eyed bug survival, individual big-eyed bugs were reared from egg hatch until death on diets of corn earworm eggs or pea aphids. Individual big-eyed bug eggs were placed in large Petri dishes (15 cm diameter) with one of the prey species. Prey were provided *ad libitum* (approximately 40 individuals) and changed every 2 days to ensure a constant supply of fresh food. The experiment was replicated 11 times. The number of days survived by each big-eyed bug was recorded and ANOVA was used to compare the longevity of big-eyed bugs fed corn earworm eggs and pea aphids.

### Prey preference

Prey density is often a confounding effect that is difficult to control in choice experiments. In an attempt to avoid density-related complications, the prey preferences of big-eyed bugs were quantified in two separate experiments. In the first experiment, prey preference was determined by comparing the consumption of focal prey in the presence and absence of alternative prey while maintaining a constant, total prey density. To quantify consumption of focal prey in the absence of alternative prey, either 40 corn earworm eggs or 40 pea aphids were placed on the uppermost leaf of a caged lima bean plant. Immature aphids were used to ensure that aphid reproduction would not alter treatment densities. A field-collected, starved, big-eyed bug adult was then released into the cage. Eighteen hours later, the cage and the big-eyed bug were removed and the numbers of consumed prey were counted. To quantify the number of focal prey consumed in the presence of alternative prey, both prey species were presented simultaneously to big-eyed bugs in the same experimental procedure as above, but 20 individuals of both prey species were provided instead of 40 individuals of one prey species. Thus, the absolute number of prey remained constant whether or not alternative prey were present (total prey density = 40).

The number of focal prey that were eaten by big-eyed bugs was recorded after 18 h. The experiment was replicated 11 times and a two-way ANOVA was used to test for effects of prey species and presence or absence of alternative prey on the number of focal prey consumed by big-eyed bugs.

In the next experiment, the density of focal prey was kept constant but not the total prey density. Twenty focal prey, either corn earworm eggs or pea aphids, were caged on a lima bean plant with a starved big-eyed bug as described above. To test for a prey preference, 20 alternative prey, either pea aphids or corn earworm eggs, respectively, were added to half the replicates. Thus, total prey density was 20 when no alternative prey were present and 40 when alternative prey were present. Each treatment combination (prey species  $\times$  presence or absence of alternative prey) was replicated 11 times and the numbers of each prey species consumed in the presence or absence of alternative prey were compared using a  $2 \times 2$  ANOVA.

### Prey mobility

The effect of prey mobility on prey selection by big-eyed bugs was assessed in two laboratory experiments. In the first experiment, partially immobilised aphids were placed in a freezer at  $-3^\circ\text{C}$  for 10 min. Ten minutes at  $-3^\circ\text{C}$  did not kill the aphids. As a result of lower body temperatures, however, these aphids were unable to walk for  $\approx 3$ –5 min. As the pea aphids warmed to room temperature, they slowly regained mobility, but did not become fully mobile for several more minutes ( $\approx 10$  min). Immediately after removal from the freezer, three immobilised pea aphids and three fully mobile pea aphids were placed on a lima bean trifoliolate in a large Petri dish (15 cm diameter) that contained one big-eyed bug. The mobile pea aphids were kept at room temperature prior to the experiment so their mobility was unimpaired. Insects were observed for 5 min and the mobility status (immobilised or mobile) of the first aphid attacked by the big-eyed bug was recorded. The replicate was stopped whenever an aphid was attacked or when immobilised aphids began to move. The experiment was replicated 40 times and the number of mobile and immobilised pea aphids attacked by big-eyed bugs was compared using a *G* test (Sokal & Rohlf, 1995). Big-eyed bugs used in this experiment were field-captured adults that were starved for 48 h prior to the experiment.

In a second experiment, the number of corn earworm eggs consumed by big-eyed bugs in the presence of mobile and immobile aphids was quantified to test the effects of alternative prey behaviour (mobile or not) on the risk of attack incurred by target prey. Aphids were immobilised by placing them in a freezer for 30 min at  $-3^\circ\text{C}$ . Freezing aphids for 30 min resulted in aphid death, but big-eyed bugs readily consumed recently frozen, moribund pea aphids in preliminary feeding trials. To quantify the number of corn earworm eggs consumed by big-eyed bugs in the presence of mobile or immobile (moribund) aphids, 20 corn earworm eggs and 20 mobile or immobile aphids were placed on a small, caged lima bean plant with a starved big-eyed bug. In this experimental design, corn

earworm eggs were the focal prey and pea aphids were the alternative prey (Holt & Lawton, 1994). Eighteen hours later, the numbers of corn earworm eggs consumed by big-eyed bugs were counted. The experiment was replicated 10 times and the numbers of corn earworm eggs consumed by big-eyed bugs in the presence of mobile and immobile aphids were compared using a one-way ANOVA (SAS Institute, 1996).

**Results**

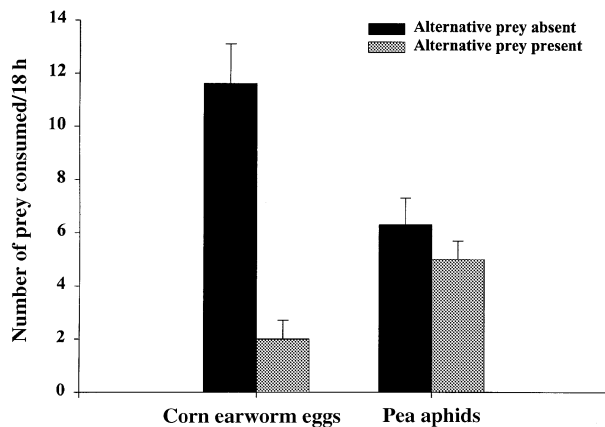
*Nutritional quality of prey*

Big-eyed bugs survived significantly longer when fed corn earworm eggs than when fed pea aphids (prey species effect,  $F_{1,20}=170.19, P<0.001$ ). The difference in survival was striking: big-eyed bugs survived almost four times as long when fed corn earworm eggs than when fed pea aphids. Big-eyed bugs fed corn earworm eggs survived an average of 60 days ( $SE \pm 9$  days) whereas bugs fed pea aphids survived an average of only  $16 \pm 5$  days. Furthermore, only big-eyed bugs that ate corn earworm eggs completed their development and reached adulthood. These results verify the nutritional superiority of corn earworm eggs over pea aphids as prey for big-eyed bugs.

**Table 1.** Analysis of variance of the effects of prey species and presence or absence of alternative prey on prey consumption by big-eyed bugs when total prey density was constant.

Source of variation	d.f.	MSE	F
Prey species	1	12.023	0.542
Alternative prey	1	290.205	13.094***
Prey species $\times$ alternative prey	1	180.023	8.122**
Error	40	22.164	

\*\*  $P<0.01$ , \*\*\*  $P<0.001$ .



**Fig. 1.** Number of corn earworm eggs and pea aphids consumed by big-eyed bugs in the presence and absence of alternative prey when the total number of prey was held constant (mean  $\pm$  SE).

*Prey preference*

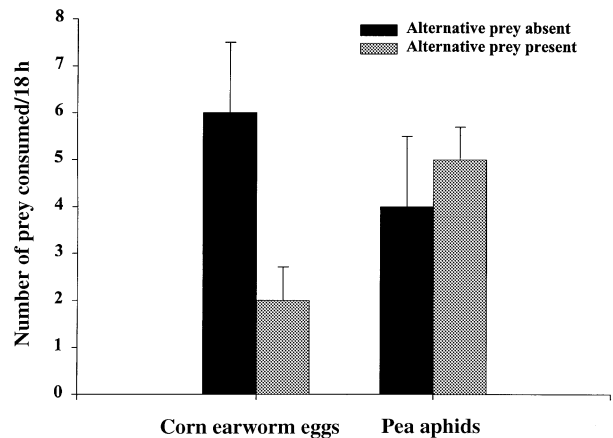
In the first prey choice experiment where total prey density remained constant, there was a significant prey species  $\times$  alternative prey interaction (Table 1). The consumption of corn earworm eggs was reduced significantly by the presence of alternative prey (pea aphids) (Fig. 1). Consumption of corn earworm eggs by big-eyed bugs dropped over fivefold when pea aphids were present, from an average of 11.18 to 2. In contrast, the consumption of pea aphids was not reduced significantly by the presence of corn earworm eggs. The number of pea aphids consumed by big-eyed bugs dropped only slightly, from an average of 6.09 to 5 when corn earworm eggs were present (Fig. 1).

A similar pattern occurred in the second choice experiment when the density of focal prey was held constant. Again, there was a significant prey species  $\times$  alternative prey interaction (Table 2). As in the first experiment, the number of corn earworm eggs consumed by big-eyed bugs decreased significantly when pea aphids were available as alternative prey (Fig. 2), however the number of pea aphids consumed by big-eyed bugs was not reduced significantly by the presence of corn earworm eggs (Fig. 2). In fact, a slight, nonsignificant increase in the number of pea aphids attacked by big-eyed bugs occurred when corn earworm eggs were present. These data

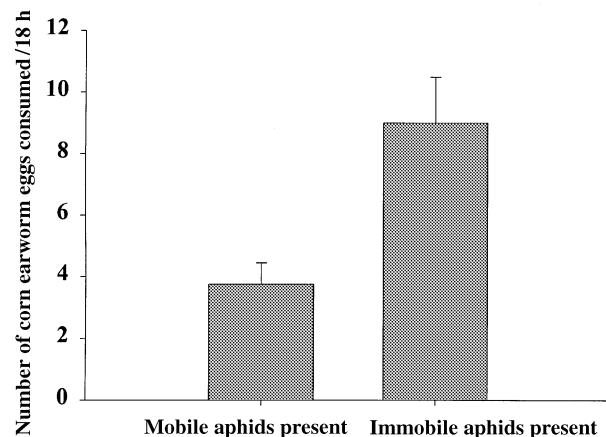
**Table 2.** Analysis of variance of the effects of prey species and presence or absence of alternative prey on prey consumption by big-eyed bugs when focal prey density was constant.

Source of variation	d.f.	MSE	F
Prey species	1	2.75	0.266
Alternative prey	1	24.75	2.391
Prey species $\times$ alternative prey	1	68.75	6.643*
Error	40	10.35	

\*  $P<0.05$ .



**Fig. 2.** Number of corn earworm eggs and pea aphids consumed by big-eyed bugs in the presence or absence of alternative prey when the number of focal prey was held constant (mean  $\pm$  SE).



**Fig. 3.** The number of corn earworm eggs that were consumed by big-eyed bugs in the presence of mobile and immobile aphids (mean  $\pm$  SE).

suggest that alternative prey can have a great effect on the risk of attack of the focal prey but that this effect can be very asymmetric depending on the prey species involved.

#### Prey mobility

Big-eyed bugs attacked fully mobile pea aphids significantly more often than partially immobile aphids. Of the 40 big-eyed bugs tested, 16 (40%) attacked an aphid during the observation period. Eleven of the 16 attacks were on mobile aphids, whereas only five immobilised aphids were attacked ( $G=4.58$ ,  $P<0.05$ ).

Moreover, the mobility of alternative prey (pea aphids) affected significantly the consumption of corn earworm eggs by big-eyed bugs. Big-eyed bugs consumed  $9.2 \pm 1.1$  corn earworm eggs per 18 h in the presence of immobilised aphids but consumed only  $3.5 \pm 1.1$  eggs when mobile aphids were the alternative prey ( $F_{1,22}=17.42$ ,  $P<0.01$ ; Fig. 3). Aphid mobility therefore had an almost threefold impact on the predation rate of corn earworm eggs by big-eyed bugs.

#### Discussion

Prey preferences of big-eyed bugs and other generalist insect predators have important consequences for predator–prey dynamics. The impact of a generalist insect predator on any given prey species depends not only on the abundance and susceptibility of that prey species but also on the abundance and susceptibility of other species that share the same enemy (Holt & Lawton, 1994). If the enemy does not prefer either prey species, the indirect effect of one prey species on the other will depend solely on the abundance of each prey species. An increase in one species will tend to relax predation pressure on the other species, and vice versa. Thus, the indirect effect of one prey species on the other as mediated by their shared

natural enemy will be symmetrical. If the enemy prefers one prey species to the other, their indirect interaction will not be symmetrical. Therefore an increase in one prey species may or may not reduce predation pressure on other prey species. This is the nature of the indirect interaction found between corn earworm eggs and pea aphids in this study. An increase in pea aphids decreased predation of corn earworm eggs by big-eyed bugs greatly but an increase in corn earworm eggs did not affect the predation of pea aphids by their shared natural enemy (Figs 1 and 2). Thus, corn earworm eggs benefited indirectly from increases in pea aphids but pea aphids did not benefit indirectly from changes in corn earworm abundance.

Understanding the prey-selection process of big-eyed bugs is key to understanding the indirect interactions between pea aphids and corn earworm eggs. Big-eyed bugs' selection of mobile prey is the mechanism that promotes a positive, indirect effect of pea aphids on corn earworm eggs. Based on these results, mobile prey species will consistently have positive, indirect effects on less mobile prey species when both prey species coexist with big-eyed bugs and other visually oriented generalist insect predators. In a previous study, the indirect effect of corn earworm eggs on pea aphids was quantified in caged field experiments that lasted one pea aphid generation (Eubanks & Denno, 1999b). The results of that relatively long-term field experiment support those reported here: the presence of corn earworm eggs as alternative prey did not reduce the impact of big-eyed bugs on pea aphid populations. These results suggest that big-eyed bugs and other visually oriented generalist insect predators may be employed more effectively against highly mobile prey species in biological control programmes or against relatively sessile prey species when more mobile prey are not abundant.

Big-eyed bugs preferentially attacked pea aphids, the nutritionally inferior prey, in both choice experiments, a surprising result (Figs 1 and 2). This study suggests that prey mobility is the primary mechanism of prey selection by big-eyed bugs. Prey selection by big-eyed bugs does not therefore correspond with predictions of optimal foraging models based on caloric consumption or models of insect diet selection based on nutrient availability (Stephens & Krebs, 1986; Bernays & Bright, 1991; Waldbauer & Friedman, 1991). Big-eyed bugs apparently do not assess the nutritional quality of their prey but instead focus their attacks selectively on mobile prey. Other studies have suggested that heteropteran predators attack and consume more mobile prey preferentially when given a choice (Rosenheim & Wilhoit, 1993; Rosenheim *et al.*, 1993). For some heteropteran predators, it is unclear whether the predator detects movement visually or through substrate-borne vibrations. Big-eyed bugs, as the name implies, have relatively large eyes and acute vision (Readio & Sweet, 1982). It is likely therefore that big-eyed bugs are visually oriented predators that react to moving prey more readily than to sessile prey. In a previous study, big-eyed bugs were able to survive extended periods when fed a mixture of nonoptimal prey and plant food (Eubanks & Denno, 1999a), suggesting that a mixed diet of nonoptimal prey and/or plant food might compensate for individual deficiencies of individual prey species (e.g. Bilde & Toft, 1997).

The results of this study highlight the potential pitfalls of using single prey species functional response experiments to estimate the impact of a generalist insect predator on a prey population. In the absence of alternative prey, big-eyed bugs do attack and consume corn earworm eggs (Eubanks & Denno, 1999a; Figs 1 and 2). When both prey species were present, however, big-eyed bugs attacked pea aphids selectively and virtually ignored the sessile corn earworm eggs. Thus, estimates of the impact of big-eyed bugs on corn earworm populations based on single species functional response experiments would grossly overestimate the real-world effect of this predator on earworm populations. Experiments that incorporate realistic combinations of alternative prey should be used to estimate the impact of generalist predators on prey populations. Despite the potential economic and ecological importance of understanding prey preferences by generalist insect predators, few studies have assessed the prey selection process of insect predators experimentally. If ecologists hope to predict the impact of generalist predators on populations or communities of prey accurately, future studies should focus on teasing apart the underlying mechanisms that determine the strength of direct and indirect interactions that occur among generalist predators and their prey assemblages (Holt & Lawton, 1994).

## References

- Araya, J.E. & Haws, B.A. (1988) Arthropod predation of black grass bugs (Hemiptera: Miridae) in Utah ranges. *Journal of Range Management*, **41**, 100–103.
- Awan, M.S. (1985) Anti-predator ploys of *Heliothis punctiger* (Lepidoptera: Noctuidae) caterpillars against the predator *Oechalia schellenbergii* (Hemiptera: Pentatomidae). *Australian Journal of Zoology*, **33**, 885–890.
- Bernays, E.A. & Bright, K.L. (1991) Inhibition of movement of larvae of the convergent lady beetle by leaf trichomes of tobacco. *Environmental Entomology*, **20**, 91–94.
- Bilde, T. & Toft, S. (1994) Prey preference and egg production of the carabid beetle *Agonum dorsale*. *Entomologia experimentalis et applicata*, **73**, 151–156.
- Bilde, T. & Toft, S. (1997) Consumption by carabid beetles of three cereal aphid species relative to other prey types. *Entomophaga*, **42**, 32.
- Champlain, R.A. & Scholdt, L.L. (1966) Rearing *Geocoris punctipes*, a lygus bug predator, in the laboratory. *Annals of the Entomological Society of America*, **59**, 1301.
- Chow, T., Long, G.E. & Tamaki, G. (1983) Effects of temperature and hunger on the functional response of *Geocoris bullatus* (Say) (Hemiptera: Lygaeidae) to *Lygus* spp. (Hemiptera: Miridae) density. *Environmental Entomology*, **12**, 1332–1338.
- de Clercq, P. & Degheele, D. (1994) Laboratory measurement of predation by *Podisus maculiventris* and *P. sagitta* (Hemiptera: Pentatomidae) on beet armyworm (Lepidoptera: Noctuidae). *Journal of Economic Entomology*, **87**, 76–83.
- Cohen, A.C. & Debolt, J.W. (1983) Rearing *Geocoris punctipes* on insect eggs. *Southwestern Entomologist*, **8**, 61–64.
- Crocker, R.L. & Whitcomb, W.H. (1980) Feeding niches of the big-eyed bugs *Geocoris bullatus*, *G. punctipes*, and *G. uliginosus* (Hemiptera: Lygaeidae: Geocorinae). *Environmental Entomology*, **9**, 508–513.
- Crocker, R.L., Whitcomb, W.H. & Ray, R.M. (1975) Effects of sex, developmental stage, and temperature on predation by *Geocoris punctipes*. *Environmental Entomology*, **4**, 531–534.
- Digweed, S.C. (1993) Selection of terrestrial gastropod prey by cychrine and pterostichine ground beetles (Coleoptera: Carabidae). *Canadian Entomologist*, **125**, 463–472.
- Eubanks, M.D. & Denno, R.F. (1999a) The ecological consequences of variation in plants and prey for an omnivorous insect. *Ecology*, **80**, 1253–1266.
- Eubanks, M.D. & Denno, R.F. (1999b) Host plants mediate omnivore–herbivore interactions and influence prey suppression. *Ecology*, in press.
- Foglar, H., Malausa, J.C. & Wajnberg, E. (1990) The functional response and preference of *Macrolophus caliginosus* (Heteroptera: Miridae) for two of its prey: *Myzus persicae* and *Tetranychus urticae*. *Entomophaga*, **35**, 465–474.
- Hagler, J.R. & Cohen, A.C. (1991) Prey selection by in vitro- and field-reared *Geocoris punctipes*. *Entomologia experimentalis et applicata*, **59**, 201–205.
- Hazzard, R.V. & Ferro, D.N. (1991) Feeding responses of adult *Coleomegilla maculata* (Coleoptera: Coccinellidae) to eggs of Colorado potato beetle (Coleoptera: Chrysomelidae) and green peach aphids (Homoptera: Aphididae). *Environmental Entomology*, **20**, 644–651.
- Heitmans, W.R.B., Overmeer, W.P.J. & van der Geest, L.P.S. (1986) The role of *Orius vicinus* Ribaut (Heteroptera: Anthracoridae) as a predator of phytophagous and predacious mites in a Dutch orchard. *Journal of Applied Entomology*, **102**, 391–402.
- Holt, R.D. (1997) Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, **12**, 197–229.
- Holt, R.D. & Lawton, J.H. (1994) The ecological consequences of shared natural enemies. *Annual Review of Ecology and Systematics*, **25**, 495–520.
- Houck, M.A. (1986) Prey preference in *Stethorus punctum* (Coleoptera: Coccinellidae). *Environmental Entomology*, **15**, 967–970.
- Izumi, S., Yano, K., Yamamoto, Y. & Takahashi, S.Y. (1994) Yolk proteins from insect eggs: structure, biosynthesis and programmed degradation during embryogenesis. *Journal of Insect Physiology*, **40**, 735–746.
- Kawooya, J.K., Osir, E.O. & Law, J.H. (1988) Uptake of the major hemolymph lipoprotein and its transformation in the insect egg. *Journal of Biological Chemistry*, **263**, 8740–8747.
- Lawrence, R.K. & Watson, T.F. (1979) Predator–prey relationship of *Geocoris punctipes* and *Heliothis virescens*. *Environmental Entomology*, **8**, 245–248.
- Loreau, M. (1983) The food regime of *Abax ater* Vill. (Coleoptera, Carabidae). *Acta Oecologica Oecologia Generalis*, **4**, 331–343.
- Mills, N.J. (1982) Voracity, cannibalism, and coccinellid predation. *Annals of Applied Biology*, **101**, 144–148.
- Nagai, K. (1991) Predatory characteristics of *Orius* sp. on *Thrips palmi* Karny, *Tetranychus kanzawai* Kishida, and *Aphis gossypii* Glover. *Japanese Journal of Applied Entomology and Zoology*, **35**, 269–274.
- Ohgushi, T. (1988) Temporal and spatial relationships between an herbivorous lady beetle *Epilachna niponica* and its predator, the earwing *Anechura harmandi*. *Research in Population Ecology*, **30**, 57–68.
- Readio, J. & Sweet, M.H. (1982) *A Review of the Geocorinae of the United States East of the 100th Meridian* (Hemiptera: Lygaeidae). Miscellaneous Publications of the Entomological Society of America, **12**, 1–91.

- Richards, L.J. (1982) Prey selection by an intertidal beetle: field test of an optimal diet model. *Oecologia*, **55**, 325–332.
- Rosenheim, J.A. & Wilhoit, L.R. (1993) Predators that eat other predators disrupt cotton aphid control. *California Agriculture*, **47**, 7–9.
- Rosenheim, J.A., Wilhoit, L.R. & Armer, C.A. (1993) Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia*, **96**, 439–449.
- SAS Institute (1996) Software Release 6.09. Cary, North Carolina.
- Siddique, A.B. & Chapman, R.B. (1987) Effect of prey type and quantity on the reproduction, development, and survival of Pacific damsel bug, *Nabis kinbergii* Reuter (Hemiptera: Nabidae). *New Zealand Journal of Zoology*, **14**, 343–349.
- Sokal, R.R. & Rohlf, F.J. (1995) *Biometry: the Principles and Practice of Statistics in Biological Research*. W.H. Freeman, New York.
- Stephens, D.W. & Krebs, J.R. (1986) *Foraging Theory*. Princeton University Press, Princeton, New Jersey.
- van Straalen, N.M. (1985) Size-specific mortality patterns in two species of forest floor Collembola. *Oecologia*, **67**, 220–223.
- Waldbauer, G.P. & Friedman, S. (1991) Self-selection of optimal diets by insects. *Annual Review of Entomology*, **36**, 43–63.
- Wyatt, T.D. & Foster, W.A. (1989) Leaving home: predation and the dispersal of larvae from the maternal burrow of *Bledius spectabilis*, a subsocial intertidal beetle. *Animal Behaviour*, **38**, 778–785.

Accepted 9 August 1999