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 Acrystosiphum 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


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 Stralen, 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,
odor, 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
\textit{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 & Degheelee, 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 \textit{et al.}, 1988; de Clercq &
Degheelee, 1994; Izumi \textit{et al.}, 1994). These same predators,
however, often attack nutritionally inferior prey species when
given a choice (Siddique & Chapman, 1987; Hagler & Cohen,

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 & Willhoit, 1993; Rosenheim \textit{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 \textit{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 preyselection 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 \textit{Geocoris punctipes} (Heteroptera: Geocoridae)
and two of its prey species, eggs of the corn earworm
Helicoverpa zea (Lepidoptera: Noctuidae) and pea aphids
\textit{Acrystosiphon 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.

\textbf{Study system}

\textbf{Predator}

Big-eyed bugs \textit{Geocoris punctipes} (Heteroptera: Geo-

coridae) 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 Lepi-
doptera (Readio & 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 \textit{et al.}, 1975;
Chow \textit{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.
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. pison* 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 × 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 × 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 °C for 10 min. Ten minutes at −3 °C did not kill the aphids. As a result of lower body temperatures, however, these aphids were unable to walk for ≈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 (≈10 min). Immediately after removal from the freezer, three immobilised pea aphids and three fully mobile pea aphids were placed on a lima bean trifoliate 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 °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.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>d.f.</th>
<th>MSE</th>
<th>$F$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prey species</td>
<td>1</td>
<td>12.023</td>
<td>0.542</td>
</tr>
<tr>
<td>Alternative prey</td>
<td>1</td>
<td>290.205</td>
<td>13.094***</td>
</tr>
<tr>
<td>Prey species $\times$ alternative prey</td>
<td>1</td>
<td>180.023</td>
<td>8.122**</td>
</tr>
<tr>
<td>Error</td>
<td>40</td>
<td>22.164</td>
<td></td>
</tr>
</tbody>
</table>

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

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.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>d.f.</th>
<th>MSE</th>
<th>$F$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prey species</td>
<td>1</td>
<td>2.75</td>
<td>0.266</td>
</tr>
<tr>
<td>Alternative prey</td>
<td>1</td>
<td>24.75</td>
<td>2.391</td>
</tr>
<tr>
<td>Prey species $\times$ alternative prey</td>
<td>1</td>
<td>68.75</td>
<td>6.643*</td>
</tr>
<tr>
<td>Error</td>
<td>40</td>
<td>10.35</td>
<td></td>
</tr>
</tbody>
</table>

* $P < 0.05$.

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).

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).
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 \((F_{1,22} = 17.42, P < 0.01; \text{Fig. 3})\). 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 \((\text{Figs 1 and 2})\). 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 \((\text{Eubanks & Denno, 1999b})\). 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 \((\text{Figs 1 and 2})\). 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 \((\text{Stephens & Krebs, 1986; Bernays & Bright, 1991; Waldbauer & Friedman, 1991})\). 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 \((\text{Rosenheim & Wilhoit, 1993; Rosenheim et al., 1993})\). 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 \((\text{Readio & Sweet, 1982})\). 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 \((\text{Eubanks & Denno, 1999a})\), suggesting that a mixed diet of nonoptimal prey and/or plant food might compensate for individual deficiencies of individual prey species \((\text{e.g. Bilde & Toft, 1997})\).
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


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.


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