THE ECOLOGICAL CONSEQUENCES OF VARIATION IN PLANTS AND PREY FOR AN OMNIVOROUS INSECT

Micky D. Eubanks[1] and Robert F. Denno

Department of Entomology, University of Maryland, College Park, Maryland 20742 USA

Abstract. We conducted a series of laboratory and field experiments to determine the effects of variation in plant quality and prey species on the survival, dispersal, and population size of a common, omnivorous insect. We also tested the hypothesis that plant feeding allows omnivorous ''predators'' to survive periods when prey are scarce. In addition, we compared the response of omnivores and strict predators to variation in plants and prey. We found that variation in plant parts (pods and leaves) and prey species (moth eggs and aphids) affected the survival, dispersal, and population size of big-eyed bugs, *Geocoris punctipes,* in Maryland lima beans. The survival of big-eyed bugs fed moth eggs was high and unaffected by the availability of lima bean pods or leaves as supplemental food. The survival of big-eyed bugs fed aphids, however, was relatively low and dramatically improved by the availability of pods. Big-eyed bugs fed only pods developed normally through the first and second instar, but development was arrested in the third instar. Only bugs fed high quality prey or mixtures of low quality prey and high quality plant food developed beyond the third instar. Plant feeding, especially pod feeding, allowed big-eyed bug nymphs to survive prey-free periods, but plant feeding was not as important for adult survival when prey were unavailable.

The dispersal of adult big-eyed bugs from lima bean plants with pods was significantly lower than the dispersal of big-eyed bugs from plants without pods. The presence of aphids on lima bean plants also reduced the dispersal of big-eyed bugs. Unexpectedly, the presence of moth eggs, high quality prey as measured by big-eyed bug survival in previous experiments, did not reduce the dispersal of big-eyed bugs.

Populations of big-eyed bugs were larger in plots of beans with pods than in plots of pod-free beans. Furthermore, the most important predictor of the density of big-eyed bugs was the number of pods per plant. Populations of other omnivorous insects (minute pirate bugs, damsel bugs, and ladybird beetles) were also larger in plots of beans with pods than in plots of pod-free beans. However, other omnivores responded to changes in the numbers of flowers per plant and not to changes in the number of pods per plant or potential prey. Conversely, the most important predictor of the density of strict, non-plant-feeding predators was the density of potential prey (herbivores).

Our results indicate that omnivory provides ecological flexibility for big-eyed bugs. Feeding at more than one trophic level furnishes big-eyed bugs with complimentary resources that allow these omnivores to survive when resources at one trophic level are of low quality (e.g., aphids) or when resources at one trophic level are totally unavailable (e.g., prey). Furthermore, the dynamics of omnivorous insects such as big-eyed bugs are intimately associated with variation in their host plants and not with changes in the density of their prey. Omnivorous insects appear to track resources at the lowest trophic level at which they feed, in this case plants, and not resources farther up the food chain (e.g., prey).

Key words: Acyrthosiphum pisum; *big-eyed bugs; corn earworm;* Geocoris punctipes; Helicoverpa zea; *lima beans; omnivory; pea aphids;* Phaseolus lunatus; *plant quality; population persistence; prey quality.*

INTRODUCTION

There is a growing awareness among ecologists that trophic interactions involving omnivores, animals that feed at more than one trophic level, are more prevalent in nature than previously supposed (Sprules and Bowerman 1988, Vadas 1989, Polis 1991, Whitman et al.

1994, Alomar and Wiedenmann 1996). As a result, authors have begun to incorporate interactions involving omnivores into current theories of population and community dynamics (Polis et al. 1989, Polis 1991, Morin and Lawler 1995, Polis and Strong 1996, Holt and Polis 1997). Because omnivores do not depend on a single resource, their population dynamics may differ markedly from those of herbivores or predators whose life histories and dynamics are strongly associated with resources at a single trophic level (Pimm and Lawton 1977, 1978, Morin and Lawler 1995, Polis and Strong

1996). Most importantly, feeding on alternative food sources may allow omnivores to persist when any single resource is scarce, potentially decoupling the dynamics of omnivores and their resources and promoting top-down control (Walde 1994, Morin and Lawler 1995, Moran et al. 1996, Polis and Strong 1996). However, models exploring the impact of omnivores or other complex consumers on community dynamics tend to assume that all resources are of equal or approximately equal value to the omnivore or consumer (Pimm and Lawton 1977, 1978, Morin and Lawler 1995, Polis and Strong 1996; but see Coll and Izraylevich 1997). This is an unrealistic assumption that contradicts the current movement to incorporate biological realism into models of food webs and community dynamics (Paine 1988, Hunter and Price 1992, Polis and Strong 1996).

Hence, a fundamental and essentially unanswered question concerning the ecological consequences of omnivory is how omnivores respond to variation in resources at more than one trophic level. For example, omnivores that feed on plants and prey encounter variation in the quality of both as food (Kiman and Yeargan 1985, Bjorndal 1991, Milne and Walter 1997). If resources at both trophic levels are roughly equivalent and essentially interchangeable, then feeding at more than one trophic level could provide omnivores with ecological flexibility by releasing these animals from a dependence on any single resource (Polis and Strong 1996). On the other hand, if resources at different trophic levels are not nutritionally equivalent, then omnivores may depend on a combination of resources and may be forced to simultaneously track resources at multiple trophic levels. Under these conditions, omnivores may be more sensitive to environmental variation than strict predators or herbivores and the hypothesized ecological flexibility associated with omnivory an illusion.

The goal of this study was to experimentally determine the effects of plant quality and prey species on the performance and population size of an omnivorous insect and to compare the response of omnivores and strict predators to variation in both plants and prey. By manipulating variation at two trophic levels, we quantified the degree of an omnivore's reliance on both prey and plant food. Furthermore, we explicitly tested the hypothesis that the ability to feed at two trophic levels promotes the population persistence of an omnivore when a resource at one trophic level is limited.

We studied a relatively simple, agricultural system consisting of an omnivorous "predator," the big-eyed bug (*Geocoris punctipes*), two of its common prey species, pea aphids (*Acyrthosiphum pisum*) and eggs of the corn earworm (*Helicoverpa zea*), and a shared host plant, lima beans (*Phaseolus lunatus*). Big-eyed bugs consume the pods and leaves of lima beans as well as pea aphids and corn earworm eggs. In turn, pea aphids and corn earworm larvae feed on the pods and leaves of lima beans. Preliminary observations and other studies of insect predation and herbivory suggest that lima bean plants and these prey species might vary in their nutritional quality as food for big-eyed bugs (Champlain and Scholdt 1966, Schumann and Todd 1982, Cohen and Debolt 1983). The specific objectives of this study were to: (1) determine the effects of variation in the presence of pods and prey species on the survival of big-eyed bugs, (2) determine if plant feeding allows big-eyed bugs to survive periods when prey are unavailable, (3) determine if the presence of pods and prey affects the dispersal of big-eyed bugs, (4) quantify the effect of pods on the population size of big-eyed bugs, and (5) compare the response of omnivores and strict predators to variation in lima beans and prey. These data represent one of the first and most comprehensive investigations of the combined effects of plants and prey on the dynamics of omnivores.

STUDY SYSTEM

Omnivores

Big-eyed bugs, *Geocoris punctipes* (Heteroptera: Lygaeidae), are abundant in lima beans, other agricultural crops, and old fields (Crocker and Whitcomb 1980). Big-eyed bugs are active in Maryland from mid-May until early October, producing three generations per year with peak densities in late July and early August. Big-eyed bugs are omnivorous, generalist "predators" and their diverse range of prey species includes aphids and lepidopteran eggs (Champlain and Scholdt 1966, Lawrence and Watson 1979, Crocker and Whitcomb 1980, Cohen and Debolt 1983). We have observed big-eyed bugs feeding on both pea aphids and corn earworm eggs in Maryland lima beans (Eubanks 1997). Big-eyed bugs also feed on the pods, seeds, and leaves of many plant species (Stoner 1970, Crocker and Whitcomb 1980, Naranjo and Stimac 1985, Thead et al. 1985). Despite their plant feeding habits, big-eyed bugs are not pests of lima beans or other agricultural plants, probably because their short proboscis and digestive enzymes do not cause extensive damage to plant tissues (Crocker and Whitcomb 1980, Nesci 1996).

Minute pirate bugs, *Orius insidiosis* (Heteroptera: Anthocoridae), are also important omnivores found in many agricultural systems, including lima beans. These tiny omnivores eat a variety of prey, including lepidopteran eggs, but also consume pollen and are strongly attracted to flowers (Kiman and Yeargan 1985, Read and Lampman 1989, Coll and Ridgeway 1995, Coll 1996). Other omnivores such as damsel bugs (*Nabis americoferus,* Heteroptera: Nabidae) and ladybird beetles (*Coleomegilla maculata* and *Coccinella septempunctata,* Coleoptera: Coccinellidae) occur in relatively small numbers. These pollen-feeding omnivores are often attracted to flowering plants and are important predators of agricultural pests (Stoner 1972, Coll and Bottrell 1991, 1992).

Host plant

Lima beans, *Phaseolus lunatus* (Leguminosae), are planted in Maryland during early summer (May and June). After 20–30 growing days, lima bean plants begin to flower and produce pods in groups of three per node on an indeterminate raceme (Wooten 1994, Nesci 1996). Plants continue to produce hundreds of pods until senescence, ~60 d after planting (Wooten 1994). The presence or absence of pods is one obvious way in which lima bean plants vary in quality for the insects that feed upon them. For example, the nitrogen content of pods is often three to five times higher than the nitrogen content of leaves (Evans 1982, Murray and Cordova-Edwards 1984, Douglas and Weaver 1989), and the performance of many insects is enhanced by feeding on pods (Schumann and Todd 1982, Mc-Williams 1983).

Strict predators

''Strict'' predators, defined here as invertebrates that essentially feed exclusively on prey, are also abundant in Maryland lima beans and feed on pea aphids, corn earworms, and other herbivores. Spiders (Thomisidae, Clubionidae, Salticidae, and Lycosidae) and assassin bugs (Heteroptera: Reduviidae) are the most abundant strict predators (Eubanks 1997). Under the most general definition of omnivory (Pimm and Lawton 1977), these animals are technically omnivores because they attack prey that occupy multiple trophic levels: other predators (intraguild predation), omnivores, and herbivores (Guillebeau and All 1989, 1990, Polis et al. 1989). Although there are a few reports of nectar drinking by crab spiders and assassin bugs (e.g., Pollard et al. 1995), these invertebrates do not eat leaves, pods, or pollen, and are almost, if not totally dependent upon prey for survival and reproduction. For example, assassin bugs received no nourishment when experimentally forced to plant feed (Stoner 1975).

Herbivores

Many species of herbivorous insects feed on Maryland lima beans and are potential prey for big-eyed bugs, other omnivores, and strict predators. Several of these species are particularly abundant and economically important, including the pea aphid, *Acyrthosiphum pisum* (Homoptera: Aphididae) and the corn earworm, *Helicoverpa zea* (Lepidoptera: Noctuidae) (Dively 1986, Nesci 1996). Pea aphids contain relatively low concentrations of nitrogen, and much of the protein content of aphids is not digestible by big-eyed bugs (Cohen 1989). Consequently, aphids are low quality prey species whose consumption by big-eyed bugs results in poor performance (Champlain and Scholdt 1966, Cohen and Debolt 1983, Cohen 1989). Corn earworm eggs contain the developing moth embryo and associated yolk and, as a result, contain extremely high concentrations of nitrogen and are often high quality prey for generalist invertebrate predators (Champlain and Scholdt 1966, Cohen and Debolt 1983).

METHODS

Effects of pods and prey species on the survival of big-eyed bugs

We conducted a 4 × 4 factorial experiment to determine if variation in plant food and prey species affected the survival of big-eyed bugs. We reared individual big-eyed bugs from egg hatch to death on 16 diets of plant and prey food. The four levels of plant food used in the experiment were lima bean leaves, lima bean pods, leaves and pods, or water soaked cotton swab (control). The four levels of prey were corn earworm eggs, pea aphids, corn earworm eggs and pea aphids, or no prey (control). We placed individual big-eyed bug eggs into large petri dishes (15 cm diameter) with plant food and/or prey. Prey were provided ad libitum (40 prey), and plant and prey were changed every 2 d to ensure that fresh food was available for big-eyed bugs throughout the experiment. Treatment combinations were replicated 11 times. We recorded the date of egg hatch, the date big-eyed bugs molted, and the number of days survived for each big-eyed bug. To fully assess the effects of variation in plants and prey on big-eyed bug survival, we measured survival two different ways. Longevity measured the absolute number of days survived by individual big-eyed bugs. Instar-specific longevity measured the absolute number of days each big-eyed bug survived within an instar. An instar ended when big-eyed bugs developed into the next instar or perished. Instar-specific longevity, therefore, was affected by both development and survival time.

Plants as alternate food for big-eyed bugs during periods of prey scarcity

To determine if plant feeding allowed big-eyed bugs to survive periods of prey scarcity, we removed prey from the diets of bugs while providing plant parts or water. We then compared the survival of these bugs with the survival of control groups that were continuously provided with prey. Because adult big-eyed bugs may be able to draw on their fat reserves during periods when prey are unavailable (Legaspi and O'Neil 1994), we conducted separate experiments to assess the role of plant food in the survival of nymphs and adults during periods without prey. Specifically, we conducted two experiments (one with nymphs, one with adults) to assess the effects of: (1) the length of the prey-free period (zero [control groups continuously provided with prey], four, or 10 d without prey), (2) the plant part provided during the prey-free period (pods and leaves, pods, leaves, or water control), and (3) the prey species consumed by big-eyed bugs prior to a period without prey (corn earworm eggs or pea aphids) on the ability of bugs to survive prey-free periods. In the first

experiment, we placed individual, third instar nymphs previously fed corn earworm eggs or pea aphids (previous prey treatment) into large petri dishes (15 cm diameter) with one of the four randomly assigned plant treatments. Nymphs in the control group were provided with the same plant part or water control as those forced to experience a prey-free period, but these bugs were constantly provided with prey. All treatment combinations were replicated nine times. At the end of the respective 4- or 10-d period, we scored bugs as alive or dead. We then compared the survival of bugs that endured prey-free periods with the survival of bugs constantly supplied with prey. In the second experiment, we repeated this protocol with newly eclosed adults previously fed corn earworm eggs or pea aphids.

Big-eyed bugs that endure prey-free periods may suffer long-term consequences as a result. The length of the period without prey, the plant food available during the period, and the prey species consumed before and after the prey-free period may interact to influence longevity. To quantify the long-term consequences of enduring a period without prey, we measured the longevity of big-eyed bug nymphs and adults that survived prey-free periods after prey were returned to their diets. Bugs fed corn earworm eggs prior to enduring prey-free periods received corn earworm eggs after enduring the period. Likewise, bugs fed pea aphids prior to enduring prey-free periods received pea aphids after the prey-free period.

Effects of pods and prey species on the dispersal of big-eyed bugs

To determine the effects of the presence of pods and prey on the dispersal of big-eyed bugs, we monitored the dispersal of adults from lima bean plants with or without prey and with or without pods. Lima bean plants used in the experiment were haphazardly selected from a 100×50 m bean field planted in June 1996 at the Central Maryland Research and Education Center in Beltsville, Prince Georges County, Maryland, USA (the field contained ~750 plants). Plants were haphazardly selected so that focal plants used in the experiment were at least 15 m apart. We marked field-collected adults on their hind tibia with a small dab of white correction fluid (Liquid Paper Brand) and starved the bugs for 24 h in the laboratory. We returned the animals to the field and caged bugs for 2 h on plants with or without 40 corn earworm eggs or 40 pea aphids and with or without pods. Bugs were caged for 2 h to allow acclimation to experimental conditions. Pods were removed by hand from focal lima bean plants (caged plants) and their four closest neighbors to establish pod-free treatments. Cages consisted of a cylinder frame of wire mesh (60 cm tall, 20 cm diameter) tightly covered with organdy cloth. We carefully removed the cages after the acclimation period and 4 h later visually searched the focal plants and their four closest neighbors. This experiment was replicated 14

times, and replicates were conducted on seven clear days during the first 3 wk of September 1996.

Effect of pods on the density of big-eyed bugs, other omnivores, and predators

To test the effects of variation in plant quality on the population size of big-eyed bugs, we manipulated the presence of pods on lima bean plants in 20×30 m field plots. Plots contained 14 rows of beans with 90 plants per row. Ten-meter strips of bare ground separated plots used in this experiment. Strips of bare ground were periodically treated with herbicide (Roundup, Monsanto, St. Louis, Missouri) and tilled. Ten plots were planted in early May (9–11 May) in Beltsville, Maryland. We applied an ethylene-based fruit thinner to five randomly selected plots on two dates to induce pod abscission (24 July and 6 August) (0.088 liter/liter of water) (Ethephon, Rhone-Poulene, Cranbury, New Jersey Ag. Co.). Ethylene-based fruit thinners, in a variety of commercial formulations, are frequently used to induce fruit abscission in fruit, cereal, and other crops (Luckwill 1977, Williams 1979). To quantify the effect of fruit-thinner applications on the number of pods per plant, we counted the number of pods on 10 randomly selected plants from each plot on six dates (22 July, 25 July, 30 July, 4 August, 15 August, and 20 August). Because fruit thinner also causes flower abscission, and many omnivorous and predaceous insects are attracted to flowering plants, we also counted the number of flowers.

To determine the long-term consequences of a reduction in pods on big-eyed bug density, we censused all plots for ~6 wk. Five suction subsamples were taken every 5–10 d, using a D-Vac suction sampler with a 0.093-m^2 orifice. Each subsample consisted of 30-s placements of the suction orifice over three plants. Collection bags were sealed and returned to the laboratory where we recorded the numbers of big-eyed bug adults, nymphs, and other insects.

To compare the response of omnivores and strict predators to variation in resources, we compared the densities of omnivores other than big-eyed bugs (minute pirate bugs, damsel bugs, and ladybird beetles), and strict predators (spiders and assassin bugs), in plots of beans with and without pods.

Statistical analyses

We assessed the effects of diet on the longevity of big-eyed bugs with a two-way ANOVA testing for effects of prey species, plant part, and their interaction. Means were compared with Bonferroni means separation test (SAS Institute 1996). Instar-specific longevity data were log-transformed and analyzed with a two-way ANOVA testing for effects of diet and instar and means were compared as above.

Logistic regression analysis allowed us to determine the effect of the length of the prey-free period, the plant part provided during the prey-free period, and previous
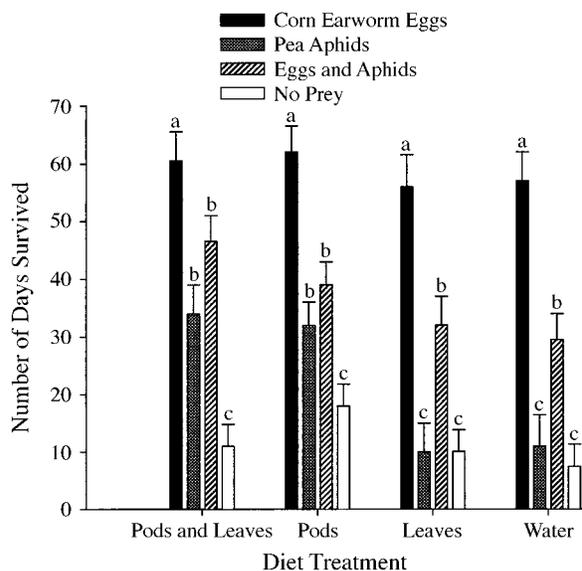
FIG. 1. Number of days survived by big-eyed bugs reared on diets containing combinations of corn earworm eggs, pea aphids, and various plant parts (mean $\pm$ 1 SE). Means with different letters are significantly different ($P < 0.05$, Bonferroni test, comparisons across all treatments).

TABLE 1. Analysis of variance for the effects of prey species and plant part on the longevity of big-eyed bugs.

Source of variation	df	MSE	F
Prey species	3	17008.28	56.15***
Plant part	3	1584.64	5.26**
Prey species $\times$ plant part	9	741.96	2.46*
Error	137	301	

   * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

of the five transformed subsample values to obtain the number of insects per plant for each plot or replicate of the experiment on each date. We compared the densities of big-eyed bugs, other omnivores, and strict predators in treated and control plots with repeated measures, one-way ANOVA. To further determine the response of insects to pod and flower loss and to changes in herbivore densities (potential prey), we calculated three multiple regressions with log-transformed big-eyed bug, other omnivore, and strict predator densities as independent variables and the number of pods per plant, the number of flowers per plant, and the number of herbivores per plant as dependent variables.

RESULTS

Effects of pods and prey species on the survival of big-eyed bugs

Prey and plant food interacted to affect big-eyed bug longevity (Fig. 1; Table 1, prey species $\times$ plant–part interaction). Big-eyed bug longevity when reared on diets containing corn earworm eggs was always higher than when fed pea aphids and independent of the plant part present (Fig. 1). In contrast, when fed pea aphids big-eyed bug survival was relatively low and signifi-
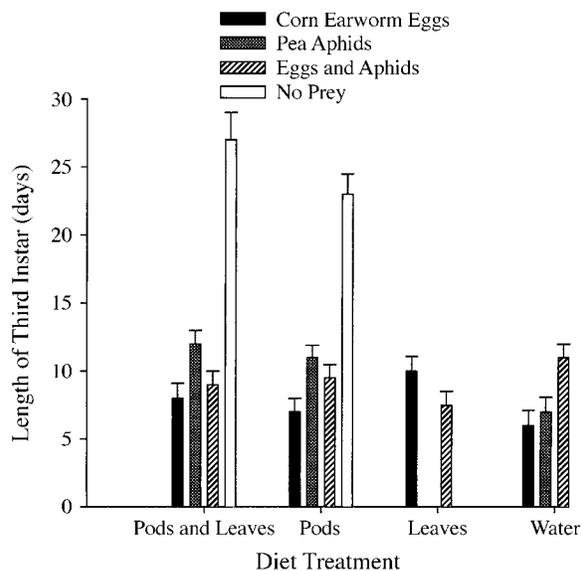
prey species on the ability of big-eyed bugs to survive periods without prey (SAS Institute 1996). We used a three-way ANOVA to determine the effects of the number of days without prey, the plant food provided during the period without prey, and the prey species consumed before and after the prey-free period on the absolute number of days survived by big-eyed bugs (longevity). Means were compared with the Bonferroni means separation test.

To determine the effects of pods and prey species on big-eyed bug dispersal, we compared the number of bugs that remained on focal or neighboring plants that had no prey, corn earworm eggs, or aphids, and the number of bugs that remained on focal or neighboring plants that had pods or did not have pods with chi-square tests (Sokal and Rohlf 1981).

We used repeated measures, one-way ANOVA to compare the numbers of pods and flowers per plant in fruit thinner-treated and control plots. We used the repeated option in the General Linear Models procedure (SAS Institute 1996) and present the Greenhouse-Geyser adjusted probabilities for F tests associated with repeated measures. Means were compared with the Bonferroni means separation test. Data were log-transformed to meet the assumptions of the analysis.

To determine the effects of pods and flower loss on the densities of big-eyed bugs, other omnivores, and strict predators, we first divided the number of insects in each subsample by three to express results as numbers of insects per plant. We log-transformed these values to meet the assumptions of ANOVA ([$\log_{10}(n + 1)$]; Sokal and Rohlf 1981). We then calculated a mean

FIG. 2. Third-instar length in days of big-eyed bugs reared on diets containing corn earworm eggs, pea aphids, and various plant parts (mean $\pm$ 1 SE).
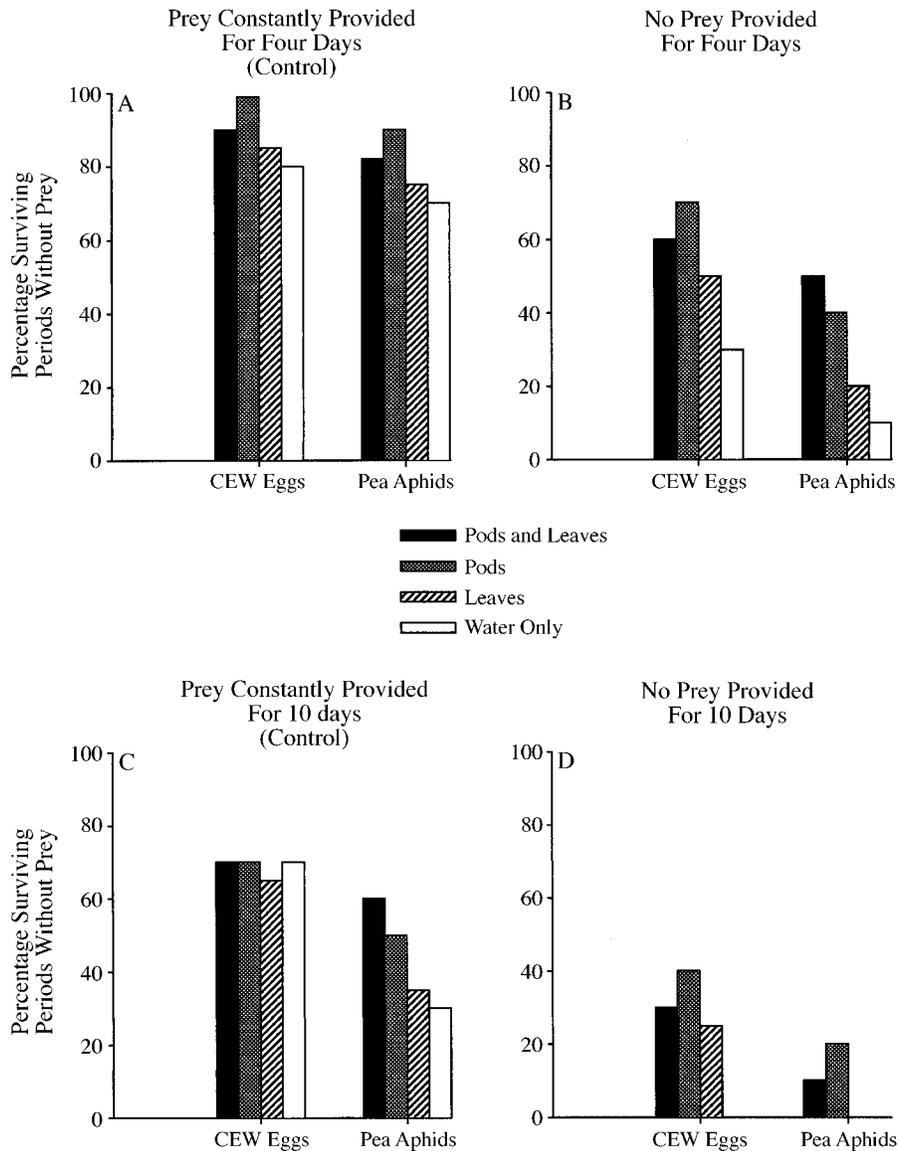
FIG. 3. Percentage of big-eyed bug nymphs that survived 4- or 10-d periods when constantly supplied with food and various plant parts (control) (A and C) or when only provided with various plant parts (B and D). CEW Eggs = corn earworm eggs.

cantly affected by the plant part present. For instance, bugs fed pea aphids and lima bean pods lived twice as long as bugs fed pea aphids and leaves, pea aphids only, or plant food only (Fig. 1). Big-eyed bug longevity on diets containing corn earworm eggs and pea aphids was intermediate of their longevity when fed either prey species alone (Fig. 1).

Bugs fed only pods developed through the first and second instar, but development was arrested in the third instar. Only big-eyed bugs fed diets containing prey developed past the third instar. The length of the third instar was significantly affected by diet (Fig. 2; diet × instar interaction, $F_{53, 498} = 8.78$, $P < 0.01$). The third

instar of bugs fed pods and no prey lasted approximately twice as long as bugs fed other diets (Fig. 2).

Plants as alternate food for big-eyed bugs during periods of prey scarcity

Nymphal survival and longevity.—Nymphal survival was adversely affected by removing prey from their diets (Figs. 3A vs. 3B and 3C vs. 3D; Table 2A, prey-free period). However, nymphs were significantly more likely to survive prey-free periods when pods were provided as food than when only leaves or water were provided as food (Fig. 3B,D; Table 2A, prey-free period × plant part interaction). Nymphs previously fed corn

TABLE 2. Logistic regression analysis for the effects of the length of prey-free periods, plant part provided, and previous prey species on the percentage of big-eyed bug (A) nymphs and (B) adults that survived prey-free periods.

Predictor	χ^2	P
A) Prey-free period	23.51	<0.01
Plant part	4.56	<0.05
Previous prey species	7.26	<0.01
Prey-free period × plant part	11.29	<0.01
Prey-free period × previous prey	3.91	<0.05
Plant part × previous prey	14.65	<0.01
Prey-free period × plant part × previous prey	1.21	>0.05
B) Prey-free period	2.76	>0.05
Plant part	3.11	>0.05
Previous prey species	2.97	>0.05
Prey-free period × plant part	1.78	>0.05
Prey-free period × previous prey	2.11	>0.05
Plant part × previous prey	7.49	<0.01
Prey-free period × plant part × previous prey	9.65	<0.01

earworm eggs were significantly more likely to survive periods without prey than nymphs previously fed pea aphids (Fig. 3B,D; Table 2A, prey-free period × previous prey interaction). For example, >50% of all nymphs previously fed corn earworm eggs survived four day periods without prey, but less than 30% of those fed pea aphids survived.

Nymphs that endured periods without prey had significantly shorter lives than those constantly provided with prey (Fig. 4A,B; Table 3A, prey-free period). The longevity of nymphs fed corn earworm eggs was only reduced by enduring ten day periods without prey (Fig. 4B), whereas the longevity of nymphs fed pea aphids was reduced by both four and ten day periods without prey (Fig. 4B; Table 3A, prey-free period × previous prey interaction). Nymphs that ate pea aphids before and after ten-day periods without prey lived longer as a result of pod feeding (Fig. 4A). However, the presence of pods did not increase the longevity of nymphs that ate corn earworm eggs before and after prey-free periods (Fig. 4B; Table 3A, prey-free period × plant part × previous prey interaction).

Adult survival and longevity.—The survival of adult big-eyed bugs was not affected by four-day periods without prey, regardless of the supplemental food that was provided (Fig. 5A vs. 5B; Table 2B). However, the survival of adults previously fed pea aphids was reduced by ten day periods when pods were not provided as supplemental food (Fig. 5D; Table 2B, prey-free period × plant part × previous prey interaction).

The lives of adult bugs that ate corn earworm eggs before and after enduring prey-free periods were longer than the lives of those that ate pea aphids (Fig. 6A,B; Table 3B, previous prey species). On average, adults fed pea aphids before enduring prey-free periods lived ~17 d after prey were returned to their diets, comparable to the longevity of adults constantly provided with pea aphids (Fig. 6A). Adults fed corn earworm eggs before enduring prey-free periods lived for ~25 d after eggs were returned to their diets, almost 70% longer than the average longevity of adults fed pea

aphids (Fig. 6B). The longevity of adults fed corn earworm eggs was not affected by 4-d periods without prey, but contrary to the results for bugs fed pea aphids, was shortened by 10-d periods (Fig. 6B; Table 3B, prey-free period × plant part × previous prey interaction).

Effects of pods and prey species on the dispersal of big-eyed bugs

Marked big-eyed bugs were significantly more likely to remain on lima bean plants with pods than on plants without pods (14 recaptures and five recaptures, respectively) ($\chi^2 = 4.26$, df = 1, $P < 0.05$). Marked big-eyed bugs were also significantly more likely to remain on lima bean plants inhabited by pea aphids than on lima bean plants inhabited by corn earworm eggs or no prey (13 recaptures, two recaptures, and four recaptures, respectively) ($\chi^2 = 10.85$, df = 2, $P < 0.01$). In all, we recaptured 19 of the 84 big-eyed bugs that we marked and released (22.6% pooled across all treatments).

Effect of pods on the density of big-eyed bugs, other omnivores, and predators

Fruit-thinner reduced the number of pods per lima bean plant by 71% within two days of application, and the number of pods per plant in treated and control plots was significantly different throughout the growing season (treatment × date interaction, $F_{1,5} = 6.83$, $P < 0.05$). Applications of fruit-thinner reduced the number of flowers per lima bean plant by 77% within two days (treatment × date interaction, $F_{1,5} = 30.91$, $P < 0.05$). Lima bean plants, however, reinitiated flowering late in the summer after the effects of the second fruit thinner application dissipated. As a result of reflowering, the number of flowers per plant was not significantly different in treated and control plots during the last few weeks of the growing season.

Densities of big-eyed bugs, other omnivores, and strict predators did not differ between control and treated plots 24 h after fruit-thinner applications (Figs. 7
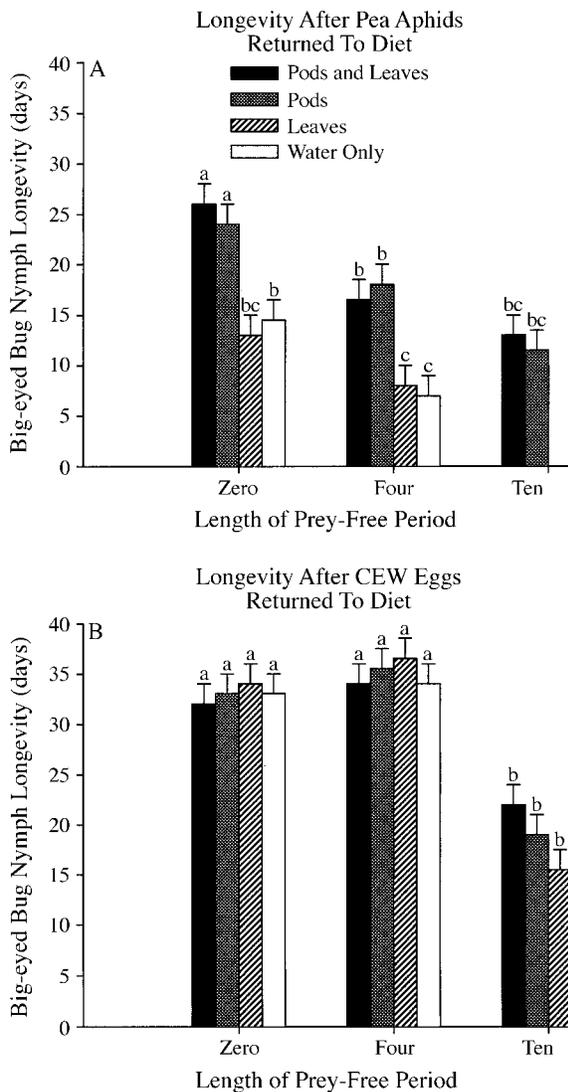
FIG. 4. Longevity of big-eyed bug nymphs that endured periods without prey after prey were returned to their diets (mean ± 1 SE). Means with different letters are significantly different ($P < 0.05$, Bonferroni test). CEW Eggs = corn earworm eggs.

and 8). Fruit thinner, therefore, did not have a direct, adverse effect on big-eyed bugs or other insects in treated plots. The loss of pods due to abscission did reduce the size of big-eyed bug populations. By the third sampling date following fruit-thinner treatment, nymphs were more abundant in plots of beans with pods than in plots of pod-free beans (Fig. 7A; date × treatment interaction for nymphs, $F_{5,40} = 4.58$, $P < 0.05$). Likewise, by the second sampling date after fruit-thinner treatment, the density of adults in plots of beans with pods was significantly higher than in plots of pod-free beans (Fig. 7B; date × treatment interaction for adults, $F_{5,40} = 6.55$, $P < 0.05$). Furthermore, variation in the number of pods per plant was the most important pre-

dictor of variation in the density of big-eyed bugs, while neither the number of flowers per plant nor herbivore density were significant predictors of big-eyed bug densities (Table 4A).

The densities of omnivorous insects other than big-eyed bugs (minute pirate bugs, damsel bugs and ladybird beetles) were significantly lower in plots of beans without pods than in plots of beans with pods (Fig. 8A; date × treatment interaction for other omnivores, $F_{5,40} = 4.02$, $P < 0.05$). The number of flowers per plant was the most important predictor of the density of these omnivores, and the number of pods per plant and herbivore density were not significant predictors (Table 4B).

The densities of strict predators were not significantly different in treated and control plots (Fig. 8B; nonsignificant date × treatment interaction for strict predators, $F_{5,40} = 0.58$, $P > 0.05$). The density of herbivores (potential prey) was the most important predictor of variation in strict predators (Table 4C). The number of pods per plant was not a significant predictor of strict predator density, but, unexpectedly, the number of flowers per plant was (Table 4C).

DISCUSSION

Effects of variation on omnivore survival

For omnivores such as big-eyed bugs, variation in the availability of plant and prey food has a dramatic effect on survival, dispersal, and population dynamics. When reared on diets containing only plant food, longevity and survivorship were higher when lima bean pods were available than when only lima bean leaves were available. Pod feeding was also important for the survival of big-eyed bugs when pea aphids were the only prey available. Bugs fed pea aphids and lima bean pods survived almost twice as long as those fed pea aphids only or pods only (Fig. 1B). Thus, big-eyed bugs benefit by diet mixing when they consume pods and pea aphids. The combination of pea aphids and lima bean pods apparently provides bugs with essential nutrients or amino acids not found in aphids or pods alone. Several studies of strict herbivores and strict predators have documented similar, positive effects of "mixed" diets on components of fitness. Feeding on mixtures of several host-plant species allows some generalist herbivores to obtain essential nutrients not found in any single plant species (Bernays and Bright 1991, Waldbauer and Friedman 1991, Bernays and Minkenberg 1997). Likewise, the survival and fecundity of generalist, invertebrate predators can be improved by consuming mixtures of prey species (Greenstone 1979, Bilde and Toft 1994, Toft 1995). Furthermore, for some vertebrate omnivores, feeding on a combination of prey and plant food can synergistically increase the value of food. For example, the caloric value of plant food was increased when ingested along with prey by an omnivorous turtle (Bjorndal 1991).

TABLE 3. Analysis of variance for the effects of the length of the prey-free period, plant part provided during period, and previous prey species on the longevity of big-eyed bug (A) nymphs and (B) adults after prey were returned to their diets.

Source of variation	df	MSE	F
A) Prey-free period	2	1359.31	115.01***
Plant part	3	333.24	28.19**
Previous prey species	1	4012.49	339.49*
Prey-free period $\times$ plant part	6	15.72	1.33
Prey-free period $\times$ previous prey	2	289.59	24.5*
Plant part $\times$ previous prey	3	159.23	13.47*
Prey-free period $\times$ plant part $\times$ previous prey	6	279.63	23.66**
Error	100	11.82	
B) Prey-free period	2	315.03	26.74**
Plant part	3	37.05	3.14*
Previous prey species	1	735.18	62.41***
Prey-free period $\times$ plant part	6	18.72	1.59
Prey-free period $\times$ previous prey	2	75.65	6.42*
Plant part $\times$ previous prey	3	41.18	3.49*
Prey-free period $\times$ plant part $\times$ previous prey	6	623.31	52.91***
Error	173	11.78	

 * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

The effects of various diets on instar-specific longevity provide further evidence for the importance of mixed diets. Nymphs fed only pods developed through the first and second instar at approximately the same rate as nymphs fed diets containing prey or prey and plant material. The third instar, however, was prolonged for bugs fed only pods, and these insects did not molt into fourth instar nymphs (Fig. 2). Thus, pods allow big-eyed bugs to reach the third instar, but their development is arrested. There appear to be key nutrient deficiencies that prevent development to the fourth instar in the absence of prey. Although pod feeding did not allow bugs to develop past the third instar, the prolonged survival of third instar bugs may allow bugs to continue development if prey become available.

Corn earworm eggs were higher quality prey for big-eyed bugs than pea aphids: both the longevity and survival of big-eyed bugs was greater when fed corn earworm eggs than when fed pea aphids. These results probably reflect differences in the nitrogen content of the two prey species. Lepidopteran eggs contain high levels of nitrogen in the developing moth embryos and associated yolk, whereas aphids contain relatively low levels of nitrogen and much of this nitrogen is not digestible by big-eyed bugs (Cohen 1989). Consequently, it is not surprising that our study and others have demonstrated that lepidopteran eggs are among the most nutritious prey for generalist insect predators and omnivores (Champlain and Scholdt 1966, Cohen and Debolt 1983, Cohen 1989).

Variation in prey species also influenced the ability of big-eyed bugs to survive periods without prey. Big-eyed bugs previously fed corn earworm eggs (high quality prey) were more likely to survive periods without prey than big-eyed bugs previously fed pea aphids (low quality prey) (Figs. 4 and 6). Furthermore, the longevity of big-eyed bugs fed corn earworm eggs before and after prey-free periods was higher than the longevity of bugs fed pea aphids (Figs. 5 and 7). The consumption of high quality prey, therefore, offsets to some extent the cost of enduring an extended period without prey. Consequently, the relative abundance of prey and the propensity of big-eyed bugs to attack high or low quality prey will affect the population dynamics of big-eyed bugs, even when prey are temporarily absent from the environment.

It appears that although the nutritional requirements of omnivorous insects may be met by a single, particularly high quality resource (e.g., moth eggs), their nutritional requirements in general are relatively complicated and diet mixing may be necessary to insure survival under a wide range of environmental conditions. When relatively high quality prey are abundant, it may be relatively easy for ecologists to predict the survival of omnivorous insects. But when high quality prey are scarce, predicting the survival of omnivorous insects will be complicated and likely require knowledge of the abundance of several prey species and the status of host plants.

Effects of variation on omnivore dispersal

The presence of pods reduced the emigration of big-eyed bugs. This result is not surprising since pods were often important for big-eyed bug survival. Big-eyed bugs located and remained on pods if they were present (M. D. Eubanks, *personal observation*), and bugs were thus less likely to leave bean plants. Variation in plant quality, therefore, strongly affected the dispersal of big-eyed bugs, and this result is consistent with studies of other omnivorous insects. Minute pirate bugs, for example, are strongly attracted to pollen and are more abundant on plants when flowers are present (Kiman and Yeargan 1985, Read and Lampman 1989, Coll and Bottrell 1991, 1992).

Because big-eyed bugs performed better when fed corn earworm eggs than when fed pea aphids, a logical
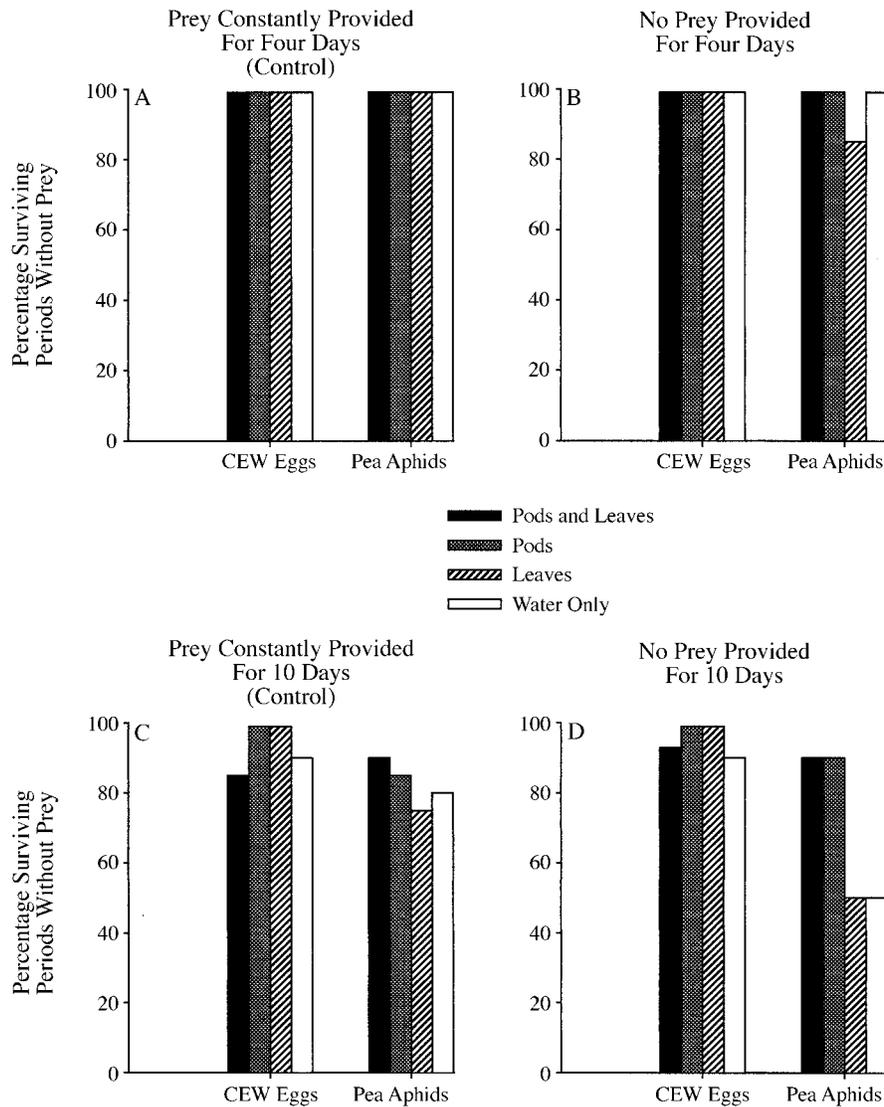
FIG. 5. Percentage of big-eyed bug adults that survived 4- or 10-d periods when constantly supplied with food and various plant parts (control) (A and C) or when only provided with various plant parts (B and D). CEW Eggs = corn earworm eggs.

prediction was that the presence of corn earworm eggs would reduce the emigration of big-eyed bugs to a greater extent than aphids. However, we observed the opposite pattern. Big-eyed bug emigration was reduced by the presence of pea aphids, but not by the presence of corn earworm eggs. An explanation of this difference requires knowledge of the foraging tactics of big-eyed bugs. In companion studies, we found that big-eyed bugs simultaneously presented with corn earworm eggs and pea aphids were significantly more likely to attack pea aphids (Eubanks 1997). Experimental manipulation of prey mobility revealed that big-eyed bugs attack mobile prey more frequently than immobile prey. It appears that big-eyed bugs are primarily visually searching predators that concentrate on moving prey. As a result, the effects of variation in resources on

dispersal may not be directly correlated with the effects of variation on survival.

Effects of variation on omnivore population size

Big-eyed bug populations were consistently larger in lima bean plots containing plants with pods than in plots containing pod-free plants (Fig. 7). Furthermore, variation in the number of pods per plant was the most important predictor of bug densities. In contrast, neither the number of flowers per plant nor herbivore density was a significant predictor of bug density. Densities of adults decreased rapidly after pod loss, suggesting that adults responded relatively quickly to changes in the abundance of pods. In contrast, the relatively slow reduction in nymphal densities suggests that nymphal survival slowly decreased in pod-free plots or that new
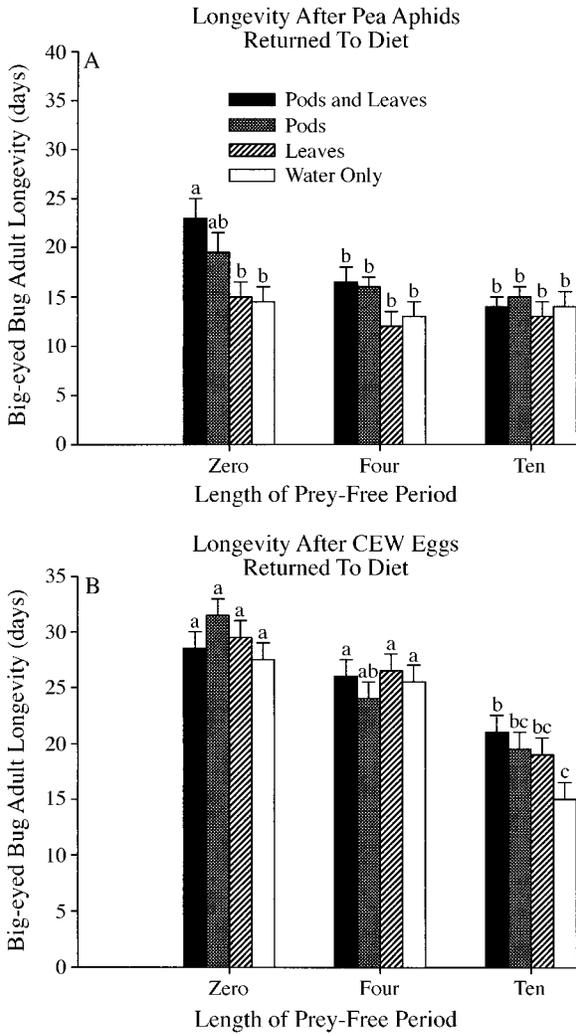
FIG. 6. Longevity of big-eyed bug adults that endured periods without prey after prey were returned to their diets (mean ± 1 SE). Means with different letters are significantly different ($P < 0.05$, Bonferroni test). CEW Eggs = corn earworm eggs.

nymphs were not recruited into the population because adult females were less abundant in pod-free plots.

The densities of omnivorous insects other than big-eyed bugs (minute pirate bugs, damsel bugs, and ladybird beetles) were also lower in pod-free plots than in control plots (Fig. 8A). However, because plants without pods flowered again late in the season, we were able to separate the effects of pods and flowers on the abundance of omnivores. Populations of these omnivores were strongly affected by the loss of flowers and not by the loss of pods or changes in herbivore densities. As previously discussed, many omnivorous insects, especially minute pirate bugs and ladybird beetles, are pollen feeders and strongly attracted to flowers. As with big-eyed bugs, variation in plant quality, flower

density in this case, played an important role in the population dynamics of these omnivores.

Effects of variation on strict predators

The density of herbivores, potential prey, was the most important predictor of variation in the abundance of strict predators. Consequently, the densities of strict predators were not significantly different in pod-free and control plots. Variation in strict predator population size was not associated with variation in the numbers of pods per plant. Surprisingly, the number of flowers per plant was a significant predictor of strict predator abundance, so variation in plants did affect these animals. There are some reports that crab spiders and assassin bugs drink nectar (e.g., Pollard et al. 1995). If this is a common behavior, then the loss of flowers and accompanying loss of nectar may have influenced predator abundance. However, there is no evidence that nectar feeding by these predators affects their survival to the degree that plant feeding affects big-eyed bugs and other omnivores (e.g., Stoner 1975, Pollard et al. 1995). We believe that the loss of prey normally attracted to flowers, an indirect effect, and not the loss of flowers themselves explains the positive association
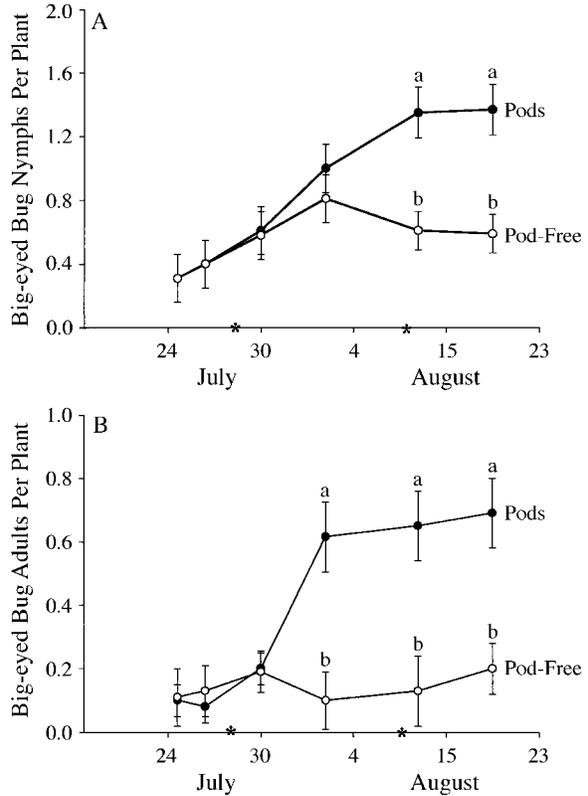

FIG. 7. Density of big-eyed bug (A) nymphs and (B) adults in control and fruit-thinner-treated lima bean plots (mean ± 1 SE). Means with different letters are significantly different ($P < 0.05$, Bonferroni test). Asterisks on the x axis indicate dates of fruit-thinner applications.
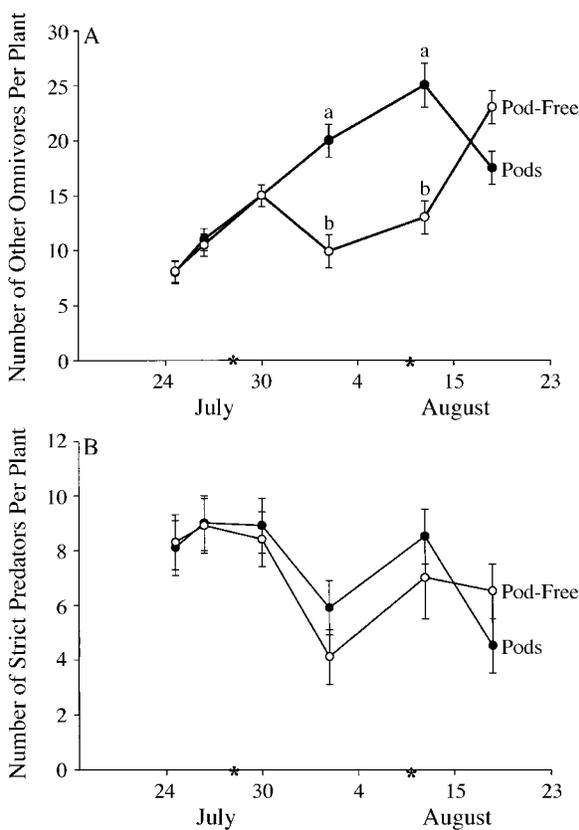
FIG. 8. Density of (A) other omnivores and (B) strict predators in control and fruit-thinner-treated lima bean plots (mean ± 1 SE). Means with different letters are significantly different ($P < 0.05$, Bonferroni test). Asterisks on the x axis indicate dates of fruit-thinner applications.

TABLE 4. The effects of the number of pods, flowers, and herbivores on (A) big-eyed bug density, (B) the density of other omnivorous insects, and (C) the density of strict, non-plant feeding predators in Maryland lima beans as ascertained with three multiple regressions.

Variable	Partial R^2	F	P
A) Pods	0.40	6.64	0.0275
Flowers	0.20	4.49	0.0630
Herbivores	0.09	2.26	0.1712
B) Pods	0.01	0.27	0.6117
Flowers	0.72	25.96	0.0005
Herbivores	0.04	1.30	0.2847
C) Pods	0.01	0.03	0.8637
Flowers	0.19	6.50	0.0312
Herbivores	0.54	11.94	0.0062

of strict predators and flowers. Both crab spiders and assassin bugs feed extensively on invertebrates attracted to flowers, including many of the omnivores that we studied (Guillebeau and All 1989, 1990, Rosenheim et al. 1995). Furthermore, other studies have documented that variation in flowering phenology influences the dynamics of crab spiders, and this effect is attributed to variation in prey abundance (Morse 1981, 1986, Morse and Fritz 1982). Overall, our comparison of the effects of variation in resources on the densities of omnivores and strict predators suggests that omnivores and strict predators have very different dynamics involving relatively complicated interactions with prey and plants.

Potential consequences for omnivore–prey interactions

Although big-eyed bug dynamics were influenced by variation in both plants and prey, our results generally support the hypothesis that feeding at multiple trophic levels provides omnivores with ecological flexibility in the form of resource options not open to strict herbivores and predators. Because big-eyed bugs feed on plants and prey, their populations are likely to be larger and persist longer than strict predators when resources vary, especially when prey densities vary (Polis and Strong 1996). Persistence of omnivores at low prey densities may decouple the dynamics of omnivores and their prey and potentially magnify the impact of omnivores on prey populations (Pimm and Lawton 1977, 1978, Walde 1994, Polis and Strong 1996). However, the potential impact of omnivores on a given prey species not only depends on the response of omnivore populations to variation in resources, but also on the extent that feeding on plants and alternative prey decreases the consumption of a particular prey species (Abrams 1987). For example, pod feeding results in relatively large and persistent big-eyed bug populations, but pod feeding might also reduce the number of prey consumed by big-eyed bugs (Abrams 1987, Eubanks 1997). Thus, the persistence afforded omnivores by feeding on multiple trophic levels may not automatically translate into enhanced suppression of prey as predicted by theory (Eubanks 1997). Nevertheless, our study demonstrates that omnivore populations can and do persist when prey are scarce and that the dynamics of omnivores and strict predators can be dramatically different.

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