Changes in the Foraging Behavior, Within-Plant Vertical Distribution, and Microhabitat Selection of a Generalist Insect Predator: an Age Analysis

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ABSTRACT The foraging behavior, within-plant vertical distribution, and microhabitat selection of 2nd instars and adults of *Zelus renardii* Kolenati were studied in an organic cotton field. In total, 47 individuals (21 nymphs and 26 adults) were observed foraging freely in the field for a total of 94 h. Both developmental stages of *Z. renardii* consumed a wide variety of arthropods including herbivores and predators, but predatory insects comprised a greater fraction of the prey of adults compared with nymphs. Adult *Z. renardii* also fed on larger prey compared with nymphs. *Z. renardii* recognized most prey from a distance, and the majority of the prey were moving when they were attacked, suggesting that this predator reacts strongly to visual stimuli. Nymphs and adults also were observed feeding on extrafloral nectaries located on the bottom of leaves and at the base of fruiting structures, Activity budgets of nymphs and adults were similar, implying no gross changes in their foraging strategies; however, nymphs spent most of their time in the lower plant strata; the adults, in contrast, foraged primarily in the upper canopy. Nymphs also spent more time on the undersurface of leaves and less time on the petioles and stems compared with the adults. These changes in within-plant vertical distribution and microhabitat selection may influence the prey encounter rates and therefore the diet composition of nymphal and adult *Z. renardii*.

KEY WORDS Hemiptera, Reduviidae, intraguild predation, ontogenetic changes, prey preference

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GENERALIST INSECT PREDATORS frequently are the most abundant natural enemies in annual agro-ecosystems. In the most extreme cases, generalist predators may consume virtually any arthropod they are able to capture. This lack of specificity allows them to establish and maintain high population densities by exploiting a variety of prey present in the field (Settle et al. 1996). Thus, generalist predators may contribute to the suppression of herbivore populations with minimal lags following the establishment of herbivore populations (Ehler 1977, Ehler and Miller 1978, Bisabri-Ershadi and Ehler 1981, Murdoch 1985, Sterling et al. 1989, Döbel and Denno 1994, Walde 1995, Settle et al. 1996).

Generalist predators may not restrict their diet to herbivore species, but rather may also feed on conspecifics or other predators. The influence of these interactions on the organization of communities has been studied in nonagricultural settings (Werner and Gilliam 1984, Sih et al. 1985, Polis et al. 1989, Wissinger and McGrady 1993). Trophic interactions between predators are important for understanding a variety of applied problems, including biological pest control in agro-ecosystems (Menge and Sutherland 1987; Moore et al. 1988; Polis et al. 1989; Power 1990; Spiller and Schoener 1990, 1994; Polis 1994; Rosenheim, 1998).

One form of predator–predator interaction is intraguild predation, which occurs when predators that share a common prey (e.g., a given herbivore) also feed on each other (Polis and McCormick 1987, Polis et al. 1989, Polis and Holt 1992, Wise 1993). Intraguild predation among generalist predators may be common in agro-ecosystems and may influence the level of herbivore population suppression. In some cases, intraguild predation may disrupt biological control (Rosenheim et al. 1993; Rosenheim et al. 1995 1998).

Upland cotton, *Gossypium hirsutum* L, is grown as an annual crop in the San Joaquin Valley of California. This crop harbors a variety of herbivore species that are exploited by a guild of generalist insect predators (van den Bosch and Hagen 1966, Ehler 1977, Ehler and Miller 1978). Since 1991, outbreaks of the cotton aphid, *Aphis gossypii* Glover, have occurred during the middle and late growing season in the presence of large populations of generalist predators, including green lacewings. Lacewings are known to be potentially important predators of aphids (Canard et al. 1984). One factor contributing to these outbreaks may be the disruption of aphid regulation by intraguild predation between lacewings and hemipteran predators (Rosenheim et al. 1993). A common and conspicuous hemipteran predator in cotton is *Zelus renardii* Kolenati (Reduviidae). *Z. renardii* is not only an important intraguild predator of lacewings and other predators (Rosenheim et al. 1993), but also shows ontogenetic changes of prey preference that influence the prevalence of intraguild predation (Cisneros and Rosenheim 1997).

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Prey preferences are measured by comparing the relative abundance of prey types in a predator's diet with the prey's abundance in the environment (Chesson 1983). Some of the components of prey preferences are prey encounter, prey recognition or detection, the choice to attack or not, prey capture, and prey consumption (Hughes 1993). Prey preference may be altered by ecological interactions with competitors and other predators (MacArthur and Levins 1967, Abrams 1983, Sih 1987, Lima and Dill 1990), by prey behavior, and by the developmental stage of the predator (Werner and Gilliam 1984).

Ontogenetic changes in prey preference have been documented for vertebrate predators (Werner and Gilliam 1984) as well as invertebrates, including arachnids (Turner 1979, Polis 1984, Hallas 1988; Lubin et al. 1991, Rayor and Uetz 1993) and insects (Fedorenko 1975, Thompson 1975, Johannsson 1978, McArdle and Lawton 1979, Lockwood 1989, Rowe 1992). The mechanisms underlying the ontogenetic changes of prey preference of some biological control agents have been studied in laboratory settings (Dixon 1970, Brown 1972, Drea 1978, Neuenschwander and Hagen 1980, Principi and Canard 1984). In these studies, the changes of prey preference have been attributed to changes in the success rate of prey capture associated with the developmental stage of the predator. Laboratory experiments generally do not, however, allow us to determine the influence that other components of prey preference (e.g., prey encounter) can have on the predator's diet. Under natural conditions, changes in how and where the different developmental stages of a predator forage may affect their prey preferences through changes in prey encounter rates (Keast 1977, Polis 1984, Ebenman 1987, Mittelbach et al. 1988, Wissinger 1988, Muotka 1990). We are not aware of any field studies in agro-ecosystems of the mechanisms underlying ontogenetic changes in prey preferences of an insect predator.

In the current study, the foraging behavior, microhabitat selection, and within-plant vertical distribution of second instars and adults of Z. *renardii* were observed under field conditions. The objective was to develop a mechanistic understanding of the changes of prey preference associated with the developmental stage of this hemipteran predator.

Materials and Methods

Direct observations of the foraging behavior, microhabitat selection, and within-plant vertical distribution of Z. *renardii* were conducted in a commercial organic cotton field between 2 and 24 August 1995 in Madera County, CA. The crop, *Gossypium hirsutum* cv. Maxxa, was maturing fruit (small bolls) at the start of the experiment.

Detailed records of the foraging behavior of a total of 47 Z. *renardii* (21 second instars and 26 adults) were made in 2-h focal observations in the field using a hand-held computer running behavioral event recording software (The Observer 3.0, Noldus Information Technology). Observations were conducted between 0800 and 1800 hours, with 2 observation sessions in the morning and 2 in the afternoon. The order of observations was rotated so that nymphs and adults were observed both in the morning and in the afternoon. The experimental unit was an individual Z. *renardii*. The treatments were 2 developmental stages of this predator (2nd instar and adult Z. *renardii*).

We selected individuals for observation by walking along plant rows, choosing a plant randomly, and searching the whole plant for Z. *renardii*. If the plant harbored <1 individual, only 1 of the insects was randomly chosen. If no Z. *renardii* were encountered, we moved down the row searching the adjacent plants until at least 1 individual was found. During our search, we tried to minimize our movements to provide as little disturbance to the predators as possible.

Once an individual was found, we waited 2–5 min to allow the insect to recover from any possible disturbance before we started the observation. Observations were made from a distance of <0.5 m. The observer stayed as motionless as possible during the observation, unless the insect moved out of view (e.g., an adult flying to a new plant), in which case the observer followed cautiously.

The information recorded for each individual included foraging behavior, within-plant vertical distribution, microhabitat selection, type of prey consumed, and net displacement.

Foraging behavior of Z. *renardii* was categorized into 5 different activities: rest, walk, ambush, feed, and groom. Each activity was defined as follows: (1) rest, the insect stays on the plant motionless with forelegs resting on the substrate, (2) walk, the insect walks from one site to another, (3) ambush, the insect waits motionless with its forelegs raised off the substrate, (4) feed, the insect ingests the prey, (5) groom, the insect cleans its antennae or other body parts with its forelegs. The time spent in each category was recorded and used to construct an activity budget.

The canopy of the cotton plant was divided into 3 vertical strata of approximately equal volumes: the upper, middle, and lower canopies. The time spent in each stratum was recorded as a measure of the within-plant vertical distribution of Z. *renardii* nymphs and adults. We recorded the time spent in each of 4 different microhabitats on the plant: the top of the leaf, the bottom of the leaf, the stem or petiole, and the fruiting structure (square, fruit or boll).

The type of prey (species identification; herbivore or predator) consumed by nymphal and adult Z. *renardii* and the time spent feeding on each prey were recorded. To avoid any disturbance in the predator's foraging behavior, we did not collect the carcasses of prey consumed by Z. *renardii*. However, we were able to record, by visual estimation, the prey developmental stage, approximate prey length (which was later corroborated with taxonomic references), the distance between the predator and prey when the predator first recognized the prey's presence (as indicated by orientation of the longitudinal axis of the predator's body toward the prey), and whether the prey was moving or stationary at the time of attack.

In addition, we recorded all incidences of Z. *renardii* recognizing potential prey and the frequency of avoidance of attack by the prey (when a potential prey moved away from a Z. *renardii* after the prey was recognized). Prey avoidance of attack sometimes seemed to be active, as evidenced by a sudden change in the prey's behavior, and at other times seemed to be passive, occurring when prey moved out of the predator's reach as a result of normal foraging. The frequency of prey escape (when a potential prey moved away from a Z. *renardii* following an unsuccessful predator attack) also was recorded. The overall percentage of attacks resulting in prey capture by nymphs and adults was estimated as ([total number of prey captured × 100%] / [total number of prey captured + total number of potential prey that escaped]). The net displacement, defined as the distance between the initial position where the individual Z. *renardii* was found and its final position at the end of the 2-h observation, was recorded along with the number of flights taken by each adult. Because individuals preparing to molt or oviposit might exhibit distinctive behavior, we wanted to assess the condition of all observed individuals. We therefore collected all observed Z. *renardii* at the end of each observation and held them in plastic containers (20-ml vials) at ambient temperature for 24 h to observe molts or oviposition. The collection of adults also was necessary to determine their sex.

The population densities of herbivorous and predatory arthropods present were quantified by samples taken at the beginning and at the end of the observations. Leaf samples ($n = 50$ fifth mainstem node leaves from the plant top) were taken to quantify densities of the dominant herbivores. Leaf samples were preserved in alcohol and washed over a fine sieve (openings 75 μm by 75 μm) in the laboratory to extract all the arthropods, and these were identified and counted using a stereomicroscope. These counts were then extrapolated to whole-plant density estimates by using a correction factor (i.e., the total number of insects found on the whole plant divided by the number found on the 5th node leaf). The correction factors were obtained from an herbivore survey conducted on whole plants in an adjacent field that had conditions similar to the study site (similar plant phenological stage, cultural practices, and degree of herbivore infestation). Whole-plant searches ($n = 20$ plants) were used to quantify the densities of immature and adult predators. The predatory arthropods observed in the whole-plant searches were identified and recorded in situ.

One-factor multivariate analysis of variance (MANOVA) tests were used to contrast the activity budgets, within-plant vertical distributions, and the microhabitat selection of nymphal and adult Z. *renardii*. For each of the tests, data were recorded as the percentage of time spent in a particular category. Logistic transformation, ln ([percentage of time spent in a particular category + 1] / [100 − percentage of time spent in the same category +1]), was used to satisfy the assumption of normality (Neter et al. 1996).

Table 1. Relative abundance (mean per leaf ± SE) of arthropods in an organic cotton field

Arthopods	50-leaf samples	20-whole plant searches
Aphis gossypii	196.3 ± 140.3	—
Tetranychus spp.[a]	59.8 ± 20.6	—
Thrips[a]	7.8 ± 2.8	—
Coccinellid egg masses	—	0.38 ± 0.13
Coccinellid larvae	—	0.45 ± 0.30
Coccinellid adults	—	0.13 ± 0.03
Geocoris nymphs	—	2.05 ± 1.45
Geocoris adults	—	1.05 ± 0.60
Nabis nymphs	—	0.87 ± 0.73
Nabis adults	—	0.20 ± 0.15
Orius nymphs	—	4.43 ± 1.28
Orius adults	—	2.28 ± 1.83
Lacewing eggs	—	4.60 ± 3.30
Lacewing larvae	—	0.75 ± 0.34
Lacewing adults	—	0.30 ± 0.25
Z. *renardii* nymphs	—	0.25 ± 0.20
Z. *renardii* adults	—	0.03 ± 0.03
Syrphid larvae	—	0.10 ± 0.05

Data shown are the averages of samples taken on 2 and 24 August 1995 in Madera County, California. —, not counted.

[a] Eggs were not included in this count.

Because the original data consisted of the proportion of time spent in each of N activity or location categories, the numbers must add up to 1.0. However, there were really only N-1 linearly independent responses; we therefore omitted 1 activity or location category from each MANOVA to ensure that each response variable was an independent measurement (Neil Willits, personal communication). If the 1-way MANOVA showed significance, 1-way ANOVA tests were conducted to see which of the dependent variables considered in the MANOVA was producing the effect. For other paired comparisons (for instance, net displacement, type of prey consumed, distance of prey recognition, percentage of prey capture success) 2-tailed t-tests were used based on untransformed data. G-tests of independence were used to compare the type of prey consumed by nymphal and adult Z. *renardii* with the type of prey available in the field.

Results

The study site harbored an outbreak population of *A. gossypii* and moderate to high densities of spider mites, *Tetranychus spp.* (Table 1). The natural enemy community was composed mainly of generalist predators associated with aphid and mite prey. These predators are very common in cotton at this time of the year. Members of the families Anthocoridae (*Orius* spp.) and Lygaeidae (*Geocoris* spp.) represented ≈76% of all predators. Green lacewing eggs also were abundant, but relative few larvae were found (Table 1). After extrapolating the herbivore densities observed on leaf samples to densities on the whole plant (counts of aphids, spider mites, and thrips on leaf samples represented 5, 11, and 2% of whole-plant densities, respectively) (J.A.R., unpublished data), the ratio of predators to herbivores was 1:295.

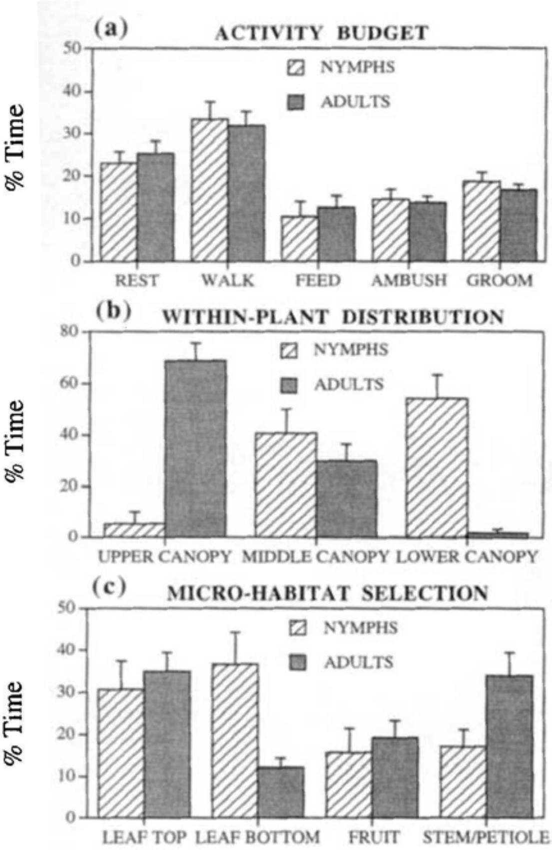

Fig. 1. Ontogenetic changes in the (a) activity budget, (b) within-plant vertical distribution, and (c) microhabitat selection of Z. *renardii*. Shown are means (±1 SE) for 2nd-instar nymphs ($n = 21$) and adult Z. *renardii* ($n = 27$) observed in 2-h samples foraging freely in the field.

Table 2. Arthropod prey consumed by 2nd-instar Z. *renardii* ($n = 21$) foraging freely in an organic cotton field

Prey	Observed frequence	Feeding time(s), mean ± SE	Approx. prey length, mm
Aphis gossypii	3	265.3 ± 197.8	1.5–1.8
Tetranychus spp.	35	127.2 ± 17.6	0.5
Coccinellid larva	12	264	3.0
Coccinellid egg mass	1	5437[a]	1.4 (per egg)
Ceocoris sp. (nymph)	1	34	2.0
Dipteran adult	1	2426	4.0

[a] Total time to feed on 6 eggs.

All nymphal Z. *renardii* ($n = 21$) were collected after the field observations, and none molted during the subsequent 24 h of captivity. Of the 27 adults observed, 22 (13 females and 9 males) were collected; the remaining 5 flew away before we could capture them and establish their sex. None of the captured females laid eggs during the subsequent 24 h. Because females and males did not show significant differences in their activity budget ($F = 2.7$; df = 3, 18; $P = 0.07$), within-plant vertical distribution ($F = 1.4$; df = 1, 20; $P = 0.24$), microhabitat selection ($F = 1.0$; df = 2, 19; $P = 0.39$), or the number of arthropod prey consumed per individual ($t = 0.67$, df = 20, $P = 0.51$), data from both sexes of adults were combined, including observations of the adults that were lost.

The activity budget of 2nd-instar Z. *renardii* was not significantly different from that of the adults (Fig. 1a; $F = 0.1$; df = 3, 43; $P = 0.96$). However, there were significant differences between nymphs and adults in within-plant vertical distribution and microhabitat selection (Fig. 1b and c; $F = 19.7$; df = 1, 45; $P < 0.001$ and $F = 5.9$; df = 2, 44; $P < 0.01$, respectively). Nymphs spent more time within the lower canopy of the plant and less time in the upper canopy compared to adults ($F = 63.4$; df = 1, 45; $P < 0.0001$, and $F = 38.9$; df = 1, 45; $P < 0.0001$, respectively). The time spent within the middle canopy of the plant by nymphs and adults was not significantly different ($F = 0.73$; df = 1, 45; $P = 0.39$). Nymphs spent significantly more time on the bottom of leaves than did the adults ($F = 9.5$; df = 1, 45; $P < 0.01$), which spent significantly more time on the stem and petioles ($F = 4.8$; df = 1, 45; $P < 0.05$). The time spent by nymphs and adults on top of the leaves and on the fruiting structures did not differ significantly ($F = 0.13$; df = 1, 45; $P = 0.73$ and $F = 1.73$; df = 1, 45; $P = 0.19$, respectively).

Nymphal and adult Z. *renardii* were observed feeding on a wide range of arthropod prey (Tables 2 and 3). The nymphal diet consisted of 7.3% predators and 92.7% herbivores ($n = 41$), whereas the adult diet consisted of 71.4% predators and 28.6% herbivores ($n = 21$). Despite the significant difference in diet composition between nymphs and adults (*G*-test of independence; $G = 27.1$, $P < 0.001$), both developmental stages showed a preference for consuming predatory arthropods; that is, the diets of both nymphal and adult Z. *renardii* were enriched for predators relative to the predator/prey ratio of 1:295 observed in the field (exact binomial probabilities; $P = 0.008$; and $P < 0.0001$, respectively).

Adults fed, on average, on larger arthropod prey than nymphs (Table 4), but consumed significantly fewer prey items. Nymphs and adults recognized most prey from a distance rather than upon physical contact (Table 4). The average distance at which prey were recognized by nymphs was significantly smaller than the average distance of recognition by adults. In addition, the majority of the prey were moving when

Table 3. Arthropod prey consumed by adult Z. *renardii* ($n = 26$) foraging freely in an organic cotton field

Prey	Observed frequency	Feeding time (s), mean ± SE	Approx. prey length, mm
Aphis gossypii	4	58.8 ± 16.4	1.5–1.8
Coccinellid larva	7	835 ± 376	3.0–9.0
Coccinellid adult	2	622 ± 578	5.0–7.0
Lacewing adult	2	1829 ± 15	13.0–19.0
Lacewing larva	1	1849	9.0
Orius tristicolor adult	2	304 ± 41	3.0
Ceocoris pallens adult	1	1881	5.0
Lepidoptera larva	1	821	10.0
Thrips	1	58	1.5

Table 4. Feeding behavior and net displacement (mean ± SE) during a 2-h focal observation of nymphal and adult *Z. renardii*

	Nymphs[a]	Adults[b]	*t*	df	*P*
No. prey consumed per individual	2.24 ± 0.38	0.81 ± 0.34	2.83	45	<0.001
Approximate prey length, mm	0.9 ± 0.2	6.9 ± 1.3	5.22	25	<0.001
Prey feeding time(s) per individual	638.6 ± 266.1	621.4 ± 191.4	0.01	45	0.31
% prey recognized from a distance	70.5 ± 10.8	73.3 ± 12.9	0.87	22	0.54
Distance of prey recognition, mm	1.8 ± 1.8	14.9 ± 2.0	4.87	16	<0.001
% prey moving when captured	89.1 ± 6.89	85.2 ± 8.59	0.35	21	0.729
Overall % success of prey capture	87.1 ± 5.16	38.9 ± 8.21	4.82	32	<0.001
No. prey recognized (orientations)	5.45 ± 0.82	5.15 ± 0.73	0.27	44	0.788
Net displacement, cm	14.1 ± 2.18	345.3 ± 100.7	2.93	43	<0.01

[a] $n = 21$.
[b] $n = 26$.

they were attacked by either nymphs or adults (Table 4). Both developmental stages had more success capturing smaller prey than larger ones (logistic regressions; $F = 7.7$; df = 1, 47; $P < 0.01$ and $F = 5.47$; df = 1, 44; $P < 0.05$, respectively). However, adult *Z. renardii* were able to capture large prey (prey range, 1.5–19.0 mm), whereas nymphs were unsuccessful capturing prey larger than 4.0 mm (Fig 2a, b). The overall percentage of attacks resulting in prey capture was higher for nymphs than adults (Table 4). All prey captured by either stage of *Z. renardii* were consumed.

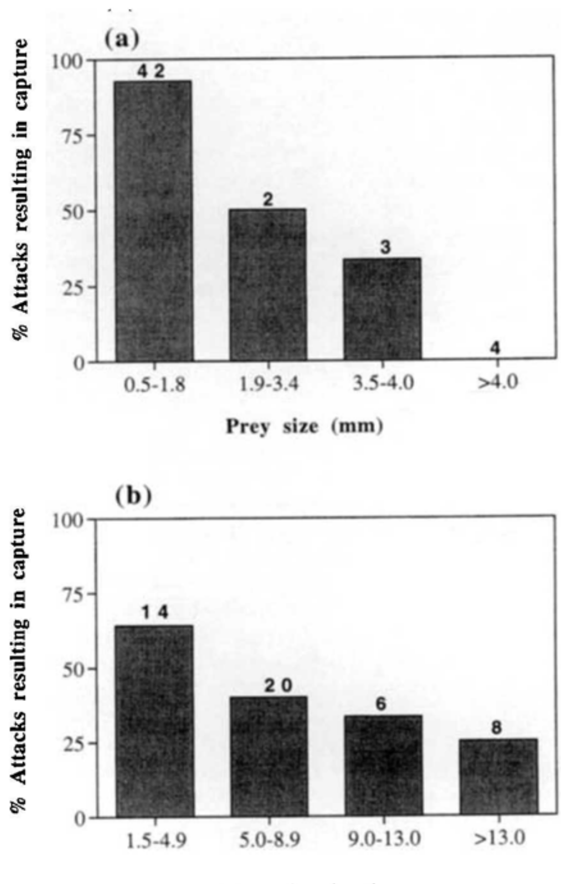

Fig. 2. Percentages of prey capture success with varying prey sizes for (a) nymphal and (b) adult *Z. renardii*. Total sample sizes (number of attacks in the indicated size range) are shown above columns.

Adult *Z. renardii* encountered more predators (indicated by the frequency of orientations toward the prey) than did the nymphs (*G*-test of independence, $G = 42.7$, $P < 0.001$). However, the relative mobility of many of these predators meant that few of these encounters led to attack and capture (Table 5). Of the total number of orientations of adult *Z. renardii* to other predatory arthropods ($n = 93$), 58.1% were toward adult stages. Nymphal *Z. renardii* encountered fewer adult predators ($G = 4.11$, $P < 0.05$) (36.6% of the orientations to predatory arthropods [$n = 30$] were toward the adult stage).

The net displacement of adults was significantly larger than the net displacement of nymphs (Table 4). In addition, a positive correlation was found between the net displacement of adults (dependent variable) and the number of flights undertaken (Fig. 3) (independent variable) ($F = 36.7$; df = 1, 23; $P < 0.0001$).

Nymphal and adult *Z. renardii* also were observed feeding on extrafloral nectaries located on the midrib on the bottom of leaves and at the base of fruiting structures. Adults fed more frequently (3.04 ± 1.14 [mean ± SE] feeding bouts per adult versus 0.24 ± 0.15 per nymph) and for greater durations (170.4 ± 70.6 s of total feeding per adult versus 6.7 ± 5.7 s per nymph) on extrafloral nectaries located at the base of fruiting structures than did nymphs ($t = 2.02$, df = 45, $P < 0.05$, and $t = 2.08$, df = 45, $P < 0.05$, respectively). No significant differences were found between adults

Table 5. Prey recognition by 2nd instar and adult *Z. renardii*

Prey type	Frequency of prey recognition (orientations)	% avoidance of attack	% of prey that escaped after attack	% of prey captured by *Z. renardii*
Zelus nymphs[a]				
Herbivores	83	50.6	3.6	45.8
Predators	25	72	20	8
Zelus adults[b]				
Herbivores	39	71.8	15.4	12.8
Predators	76	60.5	19.7	19.8
Unknown	7	71.4	28.6	0

[a] $n = 21$.
[b] $n = 26$.

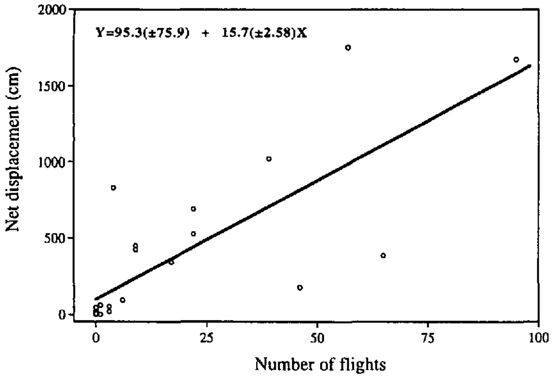

Fig. 3. Net displacement of adult Z. *renardii* ($n = 25$) plotted as a function of the frequency of flights observed per individual.

and nymphs on the feeding frequency (0.69 ± 0.21 versus 0.62 ± 0.26) and total feeding time (42.8 ± 14.8 s versus 42.5 ± 18.3 s) on extrafloral nectaries located on the midrib on the bottom of leaves ($t = 0.22$, df = 45, $P = 0.82$, and $t = 0.01$, df = 45, $P = 0.88$, respectively).

Discussion

The field where this study was conducted harbored a community of arthropods that is fairly typical for mid-season cotton grown in the San Joaquin Valley. The ratio of predators/herbivores of 1:295 is not uncommon, because the two dominant groups of herbivores, aphids and mites, have rapid population growth rates and can reach very high densities. Hemipteran predators were the most common natural enemies. Lacewings, which are considered effective biological agents of aphids, were also present, but the ratio of lacewing eggs to larvae was high. This pattern has been observed before in cotton fields (Wilson and Gutierrez 1980) and has been attributed to intraguild predation exerted by hemipteran predators on lacewing larvae (Rosenheim et al. 1993, 1998).

Our field observations demonstrated that ontogenetic changes in prey preference occur in Z. *renardii* and that the intensity of intra-guild predation on other predatory species increases with the age of this hemipteran predator, corroborating the results of our previous field experiments (Cisneros and Rosenheim 1997). Both developmental stages consumed herbivorous and predatory arthropods; however, Z. *renardii* adults fed on larger prey and on a greater proportion of predatory species than did 2nd instars.

These ontogenetic changes in prey preference do not appear to be attributable to differences in the activity budget or foraging behavior of nymphs and adults. Both nymphs and adults exhibited similar activity budgets (Fig. 1a), recognized most prey at a distance, and attacked primarily moving prey (Table 4). However, the within-plant vertical distributions of nymphs and adults were different (Fig. 1b). Nymphs occupied the lower stratum of the plant, whereas adults spent most of their time in the upper plant stratum. This pattern of vertical distribution, in which adults tend to be concentrated in the upper plant strata and immatures in the lower plant strata, also has been observed with other predatory arthropods on cotton (Wilson and Gutierrez 1980) and soybeans (Braman and Yeargan 1989) and has been described as a mechanism of avoiding cannibalism. These differences in the use of plant strata by nymphs and adults of Z. *renardii* also may generate differences in prey-encounter rates. Adults of this hemipteran predator may encounter more frequently older stages of other predatory species, whereas Z. *renardii* nymphs may encounter more frequently younger stages of these predators. These inferences are supported by our field observations, in which the potential prey recognized by adult Z. *renardii* were mainly adults of other predators, whereas nymphal Z. *renardii* encountered mostly immatures of these predatory species.

The young nymphs of Z. *renardii* also spent more time on the undersurface of leaves than the adults. This difference in microhabitat selection also may influence prey encounter rates. The predominant herbivorous arthropods present at our study site, aphids and spider mites, feed mainly on the undersurface of the leaves; thus, aphids and mites may be more likely to be encountered by nymphal rather than adult Z. *renardii*. The diet of the nymphal and adult Z. *renardii* recorded during these behavioral observations are consistent with these inferences (Tables 2 and 3).

Even though changes in prey encounter rate associated with changes in within-plant vertical distribution and microhabitat selection may be an important component of the ontogenetic changes in prey preference of this predator, the ability to recognize and capture prey also seem to play an important role. The young nymphs of Z. *renardii* did not capture prey longer than 4 mm (Fig. 2a), which included the older stages of other predators, but were able to recognize and consume prey as short as 0.5 mm. The prey consumed by adult Z. *renardii* ranged from 1.5 to 19 mm in length. It is not surprising that the adult Z. *renardii* fed, on average, on larger prey than the 2nd instars (Table 3); similar patterns also have been observed for other predatory species in which larger predators consume larger prey (Hespenheide 1973). Adult Z. *renardii* did not consume prey shorter than 1.5 mm (Fig. 2b). Optimal diet theory predicts that potential prey may be excluded from the diet if the energy gain is not sufficiently large relative to the energetic or time costs (or both) incurred in prey capture and consumption; therefore, prey smaller than a certain size may be rejected by the predator. From our observations, it is not possible to determine if adult Z. *renardii* were unable to recognize prey smaller than 1.5 mm or if they just ignored them.

Both developmental stages of Z. *renardii*, 2nd instars and adults, detected most of their prey from a distance (Table 4), and most of the prey were moving when they were captured by Z. *renardii*, suggesting that movement plays an important role in the detection of prey. Many predatory reduviids react strongly to both olfactory and moving visual stimuli (Parker 1965, 1969, 1971, 1972; Haridass and Ananthakrishnan 1980; Ambrose et al. 1991; Ambrose and Mayamuthu 1994). Ables (1978) suggested that the diet of *Z. renardii* is strongly dependent upon the relative abundance of the different types of available prey. However, our observations suggest that preferences, potentially influenced by prey recognition, also may be critically important. *Z. renardii* responded strongly to prey movement, and the lack of movement in the relatively sessile cotton aphid may explain why *Z. renardii* only rarely consumed these abundant prey (Table 1). In fact, in all the cases where aphids were consumed by either stage of *Z. renardii*, the prey were walking when they were attacked.

In addition to consuming a wide range of arthropod prey, 2nd instar and adult *Z. renardii* were observed feeding on extra-floral nectaries located on the bottom of leaves and at the base of fruiting structures. Nectivory as well as feeding on plant tissue or pollen have been observed in other predaceous hemipterans, and have been shown in many cases to be of nutritional value for both immatures and adults (Naranjo and Gibson 1996). Further studies need to be conducted to determine the function of the extrafloral nectar feeding habits of *Z. renardii*.

In conclusion, our observations suggest that to understand predator–predator interactions and the role of predation in the regulation of herbivore populations, it may be critical to measure the behavior of both nymphal and adult stages of generalist insect predators. The significant differences in the effects of nymphal and adult *Z. renardii* that were observed in manipulative experiments (Cisneros and Rosenheim 1997) appear to be based at least in part on important differences in microhabitat selection and within-plant vertical distributions of these different life stages.

Future studies with this generalist predator could focus on the implications of ontogenetic habitat partitioning for the population dynamics of *Z. renardii* and its prey. In addition, further work is necessary to determine if abiotic (temperature, humidity, light intensity) or biotic factors (prey availability, cannibalism or predation risk avoidance) contribute to these ontogenetic changes in within-plant vertical distribution and microhabitat selection.

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