

Effect of Two Prey Types on Life-History Characteristics and Predation Rate of *Geocoris floridanus* (Heteroptera: Geocoridae)

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Environ. Entomol. 33(4): 964–974 (2004)

ABSTRACT The predator *Geocoris floridanus* Blatchley has become more common in row crop systems in Georgia, but its ecology is unknown. We studied selected life-history characteristics of *G. floridanus* in the laboratory. Two prey treatments were evaluated for nymphs and adults of *G. floridanus*: 1) eggs of the corn earworm, *Helicoverpa zea* (Boddie), and (2) young larvae of the beet armyworm, *Spodoptera exigua* (Hübner). *G. floridanus* nymphs were reared on the prey, and predator development and prey consumption were monitored; predation rates, longevity, and fecundity of adults were evaluated. Nymphal development times and number of prey consumed by predators fed corn earworm eggs were similar for females and males. Nymphal development of predators fed beet armyworm larvae was prolonged compared with predators reared on corn earworm eggs. Nymphal survival was unaffected by prey type. Nymphs reared on corn earworm eggs required fewer prey to complete nymphal development and produced larger adults. Females fed corn earworm eggs had shorter preoviposition periods, and greater fecundity and longevity than females fed beet armyworms. Females consumed more beet armyworms than corn earworm eggs, but produced fewer eggs per unit prey. Female predators fed beet armyworms while nymphs and switched to corn earworm eggs when adult partially recovered their fecundity, and exhibited life-history characteristics equal to those of females fed corn earworm eggs throughout their lives. Thus, *G. floridanus* can feed, develop, and reproduce on both prey species, and its performance increases when switched from beet armyworm larvae to corn earworm eggs.

KEY WORDS big-eyed bug, life table, *Helicoverpa zea*, *Spodoptera exigua*, generalist predator

THE SUBFAMILY GEOCORINAE WAS recently elevated to the family Geocoridae with 14 described genera (Henry 1997). The principal genus *Geocoris* is worldwide in distribution, including 124 described species (Readio and Sweet 1982). Known as big-eyed bugs, they are common and naturally occurring predators of various arthropod pests in different crop ecosystems of the United States and other countries.

Several species of big-eyed bug are polyphagous predators of economic importance (Sweet 2000). Long lists of prey species are provided by Tamaki and Weeks (1972) and Crocker and Whitcomb (1980) for *Geocoris* spp., including prey from at least 3 classes, 10 orders, and 30 families of arthropods. Despite their apparent lack of prey discrimination, the development and reproduction of these generalist predators can be greatly influenced by the relative quality of the prey. Dunbar and Bacon (1972) reported high variability in the rates of development, survival, and reproduction of *Geocoris punctipes* (Say) when fed with a variety of prey species in laboratory. Despite a wide prey range,

G. punctipes displayed a higher survivorship, shorter development period, higher fecundity, and other life-history benefits when it consumed lepidopteran eggs relative to other prey items (Dunbar and Bacon 1972, Cohen and DeBolt 1983). Therefore, data on predation, development, and reproduction of big-eyed bugs on different prey can provide valuable insights into ecological attributes of these predators, such as prey suitability and preference, potential predator population dynamics relative to particular pests, and potential for biological control.

Although there is considerable biological information available for *Geocoris* spp., there is nothing known about the biology of *Geocoris floridanus* Blatchley, a species that has recently been found increasingly in cotton fields in Georgia. *G. floridanus* was originally described as a variety of *Geocoris bullatus* (Say) by Blatchley (1926), but it has since been recognized as a distinct species (Readio and Sweet 1982). It occurs in the southern United States, ranging from East Texas to Florida and north to Washington DC, although Georgia and Florida appear to be the center of distribution (Readio and Sweet 1982). *G. floridanus* is a typical geocorid in appearance, and is predominantly found on the ground or on low-growing foliage. All

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previously reported collections and observations were made on specimens in open sandy areas and grassy areas (Radio and Sweet 1982) and on the ground (Stuart et al. 2003), as was the case with our original collections in the tobacco fields at the Coastal Plain Experimental Station (Tifton, GA). However, recent collections have been made in different cotton fields near Tifton, Georgia, in drop cloth samples (our unpublished data). The small size of *G. floridanus*, its agile behavior and capacity to disappear rapidly in debris and soil crevices, overall dull coloration, and superficial resemblance to other Southeastern United States species (most notably *G. punctipes*) may contribute to an underestimation of the abundance of this species. In a recent review covering the economic importance of big-eyed bugs by Sweet (2000), no references were made to *G. floridanus*. Given the lack of information on this species, this experiment was conducted to investigate the developmental, reproductive, and predation rates of *G. floridanus* under laboratory conditions using two prey types of economic importance. Given the possible increasing presence of this species in crop systems, it is important to understand its ecology and its potential for impact on target pests.

Materials and Methods

Acquisition and Maintenance of Insects. Adults (two males and four females) of *G. floridanus* were collected in May 2001 from a tobacco field infested by aphids on the Coastal Plain Experiment Station (CPES) of the University of Georgia (Tifton, GA), where the predator occurred in combination with *G. punctipes* and *Geocoris uliginosus* (Say). Adult males and females were brought to the laboratory and reared in 1-pint paper containers (Neptune Paper Products, Newark, NJ) provided with a square of cotton batting for oviposition, corn earworm eggs for food, and a section of green bean pod for moisture. All bugs were held in environmentally controlled chambers at $26 \pm 1^\circ\text{C}$, $60 \pm 5\%$ RH, and a photoperiod of 14:10 (L:D) for rearing and for all experiments.

Nymphal Developmental Time, Survival, and Predation. In this study, we used first-generation offspring of the field-collected female and male *G. floridanus*. Newly eclosed nymphs were held individually in 33-ml plastic cups containing a piece of cheesecloth ($\approx 1\text{ cm}^2$) as a mobility substrate, and were provided with sections of green bean (*Phaseolus vulgaris* L.) pods for moisture and the designated prey items daily (see below). The cup was closed using a paper disc lid. Two prey treatments were compared: 1) eggs of the corn earworm, *Helicoverpa zea* (Boddie), and 2) neonate larvae ($<12\text{ h}$ posteclosion) of the beet armyworm, *Spodoptera exigua* (Hübner). Eggs of the corn earworm are a high-quality prey for *G. punctipes*, fostering rapid development and high survival and fecundity; we assumed that there would be a similar result with *G. floridanus*. In contrast, preliminary observations with beet armyworm larvae indicated that they were not as suitable prey for development and

reproduction of *G. punctipes* as were corn earworm eggs (our unpublished data), and we extrapolated these observations to *G. floridanus* to provide a comparison of diets. Groups of corn earworm larvae could not be used in the tests because they are highly cannibalistic, and this would have seriously confounded our results. Eggs of beet armyworm also were not used because beet armyworm egg masses are covered with a thick layer of moth scales that interfere with the foraging capability of the predators. Beet armyworm larvae, however, are not cannibalistic and are often found in groups in the field, where they are attacked by *Geocoris* species (Ruberson et al. 1994).

Nymphal development and number of prey consumed were measured daily for 66 nymphs in each prey treatment. Daily prey numbers were adjusted for predator stadium: 4, 6, 8, 12, and 20 corn earworm eggs or beet armyworm neonates were provided to the first, second, third, fourth, and fifth instars, respectively. Simultaneously, a treatment composed of four replications for beet armyworm neonates alone (no predators in the cups) at the same densities offered to the nymphs was set up to evaluate natural mortality of these larvae during the 24-h exposure period, to correct for nonpredation mortality throughout nymphal development. Nymphal development times, mortality, and predation for each stadium (number of prey consumed per day), as well as the gender of emerged adults, were monitored. The average number of beet armyworm larvae dying in the controls (i.e., without exposure to predators) was found to be 0.33, 1.5, 1.83, 2.3, and 2.33 per day at each density offered to nymphs during the respective five instars of *G. floridanus*, and these values were used to compute the real daily mortality of beet armyworm larvae caused by predation. Corrected values were used in the analyses of nymphal predation rate. Predation of corn earworm eggs was determined using a magnifying lamp ($\times 10$) to count the number of intact eggs remaining after 24 h. Preyed corn earworm eggs consisted of only pieces of egg chorion and/or were totally collapsed. Predated eggs were readily distinguished from eggs that were not attacked.

Adult Survival, Reproduction, and Predation. Newly emerged adult *G. floridanus* were held individually and fed the same prey regimen as that received during the nymphal period. To study adult predation and reproduction in relation to prey diet, 20 3-d-old females were paired with males for each prey type, and pairs were individually held in 500-ml paper containers covered with organdy cloth. The remaining adults reared on beet armyworm larvae were paired ($n = 6$ pairs) and switched after pairing (when 3 d old) to corn earworm eggs as prey for the duration of their adult lives. Females arising from nymphs fed corn earworm eggs are hereafter called corn earworm females; females fed beet armyworm larvae will be referred to as beet armyworm females; and females fed beet armyworm larvae when nymphs and corn earworm eggs when adult are called beet armyworm-corn earworm females. Prey were introduced daily at the rate of 40 corn earworm eggs or 40 beet armyworm

larvae (2 d old and fed 1 d on artificial diet) per pair of bugs. A section of green bean pod ≈ 1 cm long was introduced daily for moisture, and a piece of white cotton batting (≈ 1 cm²) was provided daily for oviposition. Prey consumed, oviposition, and predator mortality were scored daily. Besides on the cotton squares, eggs also were sometimes located at the bottom edge of the paper containers and sometimes on the organdy cloth. All eggs collected in a single day were held together in plastic cups with a section of green bean, to determine egg viability (and, thereby, female fertility) and egg incubation period.

Adult Body Size. Effects of nymphal food on the size of adult males and females were evaluated through two 2-dimensional measurements: head size (the distance from the anterior tip of the head to the occipital suture and the interocular distance measured between ocular sulci) and pronotum size (the length along the middle line of the pronotum and the width at the posterior margin of the pronotum). These measurements were obtained after the death of the bugs used to establish the adult reproductive parameters. Measurements were taken using a stereomicroscope equipped with an ocular micrometer calibrated to millimeters after correction.

Voucher specimens of the insects studied in this work are deposited at the Natural History Museum, University of Georgia Collection of Arthropods.

Data Analysis. Nymphal development and consumption rates, adult reproductive parameters (age of female at first oviposition, egg incubation period, reproductive period from first to last oviposition, female longevity, eggs produced per day of reproductive period, number of eggs per female, apparent female fertility measured by percentage of eggs hatching, number of eggs deposited per prey item consumed, total number of prey consumed), and adult male and female size were submitted to the Levene's test for homogeneity of variance (Snedecor and Cochran 1980). Predation rate for fourth-instar nymphs, age of female at first oviposition, number of eggs per female, and number of eggs deposited per prey item consumed were transformed (square root [$x + 0.5$]) to fit analysis of variance (ANOVA) assumptions. The data were analyzed using ANOVA, and significant means were separated using Tukey's honestly significant difference test at 0.05 significance levels. Results from virgin adult female and male predation rate and body size were analyzed by two-way ANOVA, considering prey items and gender as factors after verifying homogeneity of variance with Levene's test. Nymphal mortality, within instars and throughout nymphal development, was analyzed using a χ^2 test of significance. The egg incubation period and female fertility, nymphal duration and survivorship, female survival, daily female egg production, fertility, and population sex ratio data for each treatment were used to estimate the life table parameters: net reproductive rate (R_0), mean generation time (T), intrinsic rate of population increase (r_m), finite rate of increase (λ), and population doubling time (DT), according to the methods described in Birch (1948). To perform statistical in-

ferences on r_m , the variance was assessed using the jackknife methods described by Meyer et al. (1986). The obtained life table values, with exception of DT, were submitted to the Levene's test for homogeneity of variance, and no transformation was required to run the ANOVA. The data on nymphal developmental times and survivorship, and emergent sex ratio used to estimate the life table parameters for beet armyworm-corn earworm females were the same as those obtained from nymphs fed beet armyworm neonate larvae, because they were maintained on the same prey diet during their nymphal stadia. All analysis and mean comparisons were performed using the PROC GLM for unbalanced designs in the SAS statistical package (SAS Institute 1999).

Results

Nymphal Developmental Time, Survival, and Predation. *G. floridanus* nymphs fed corn earworm eggs developed more rapidly than nymphs fed beet armyworm larvae (Table 1). Nymphs fed corn earworm eggs developed through each instar ≈ 1 d faster, and the overall duration of the nymphal period was 4 d shorter for bugs fed corn earworm eggs compared with those fed beet armyworm larvae (see Table 1 for statistics). The sex ratio (number of females/total of adults) of emerging adults did not differ between prey treatments: 0.45 and 0.5 for nymphs fed corn earworm eggs and beet armyworm larvae, respectively.

Mean mortality of *G. floridanus* nymphs in both prey treatments was relatively low: mortality from egg to adult was 19.7% for nymphs fed corn earworm eggs and 21.2% for nymphs fed beet armyworm neonates (Fig. 1). Mortality of nymphs occurred only during the first three instars in both food treatments. In addition, no significant difference in stage-specific nymphal mortality was found between prey treatments (first instar, $df = 1$, $\chi^2 = 0.971$, $P = 0.6164$; second instar, $df = 1$, $\chi^2 = 2.3397$, $P = 0.2098$; and third instar, $df = 1$, $\chi^2 = 2.3459$, $P = 0.2072$) or for the complete nymphal period ($df = 1$, $\chi^2 = 0.6078$, $P = 0.7245$; Fig. 1).

Averaging the number of prey consumed during all nymphal stadia, ≈ 100 corn earworm eggs and 125 beet armyworm neonates were consumed by *G. floridanus* nymphs (Table 2) in the respective prey treatments. From the first to the third instar, *G. floridanus* nymphs exhibited similar predation rates on corn earworm eggs and beet armyworm neonates; however, predation on beet armyworm larvae was greater than on corn earworm eggs during the predators' fourth ($df = 1$, 103; $F = 6.11$; $P < 0.0001$) and fifth instars ($df = 1$, 103; $F = 40.5$; $P < 0.0001$) (Table 2). Within prey treatments, no differences were observed in the number of prey consumed by male or female predators (Table 2 and statistics therein). Cumulatively throughout their preimaginal development, female and male bugs consumed more beet armyworm neonate larvae than corn earworm eggs.

Adult Survival, Reproduction, and Predation. All females fed corn earworm eggs produced eggs; one

Table 1. Mean (± SE) developmental time (d) for each instar and from first instar to adult of *G. floridanus* reared on *H. zea* eggs (corn earworm) and 1-day-old larvae of *S. exigua* (beet armyworm) (26 ± 1°C, L:D = 14:10)

Prey	1st instar	2nd instar	3rd instar	4th instar	5th instar	Female	Male	Gender effect
corn earworm n	4.3 ± 0.12 57	3.5 ± 0.08 55	3.5 ± 0.11 54	3.8 ± 0.08 53	5.1 ± 0.12 53	19.4 ± 0.21 24	21.1 ± 0.30 29	$F_{1,51} = 19.21^{***}$
beet armyworm n	4.9 ± 0.16 60	4.3 ± 0.12 55	4.3 ± 0.14 52	4.6 ± 0.09 52	6.5 ± 0.09 52	24.2 ± 0.30 26	25.2 ± 0.48 26	$F_{1,50} = 2.67^{ns}$
Statistics	$F_{1,115} = 7.67^{**}$	$F_{1,108} = 27.9^{***}$	$F_{1,104} = 23.1^{***}$	$F_{1,103} = 82.9^{***}$	$F_{1,103} = 96.6^{***}$	$F_{1,48} = 174.2^{***}$	$F_{1,53} = 52.1^{***}$	

***P < 0.001, **P < 0.0001.

female was lost at the ninth day of adult life and she was omitted from the analysis. Thus, 19 females were used for analyzing adult reproduction and predation, and to estimate fertility life table parameters for bugs fed corn earworm. Results from females fed beet armyworm larvae were variable: four females were omitted from analysis; these four females produced fewer than 15 eggs (4.2 times fewer than the standard deviation for the whole population average), and two of those females produced nonviable eggs. Thus, 16 of 20 females fed beet armyworm larvae were used in the final analysis.

The first egg batch produced by predator females fed corn earworm, beet armyworm-corn earworm, and beet armyworm only was ≈5, 5.5, and 11 d after adult emergence, respectively. Corn earworm and beet armyworm-corn earworm females generally initiated oviposition sooner than females fed only beet armyworm (df = 2, 38; $F = 25.52$; $P < 0.0001$; Table 3). The egg incubation period was comparable among treatments (df = 1, 38; $F = 1.01$; $P = 0.3174$), as was egg viability (df = 2, 38; $F = 0.01$; $P = 0.9892$), although viability was highly variable (23–100%).

A significant effect of prey items on *G. floridanus* fecundity was observed (Table 3). The corn earworm females produced the most eggs (df = 1, 38; $F = 71.87$; $P < 0.0001$), followed by beet armyworm-corn earworm females and beet armyworm females. A similar sequence of treatments was observed for daily egg production and reproductive period. The corn earworm females produced the greatest number of eggs per day, followed by beet armyworm-corn earworm females and beet armyworm females (df = 2, 38; $F = 22.26$; $P < 0.0001$) (Table 3). Similarly, corn earworm females also persisted in laying eggs for a longer period (reproductive period, df = 2, 38; $F = 16.09$; $P < 0.0001$) than beet armyworm-corn earworm and beet armyworm females (Table 3). Peak production of eggs yielding female offspring (mx) occurred from the second to third weeks in all treatments (Fig. 2); however, the magnitude of the peak was numerically higher for females fed corn earworm (2.39 females [mx]/female/day) and beet armyworm-corn earworm (3.08 females [mx]/female/day) than for those fed only beet armyworm (1.1 females [mx]/female/day) (Fig. 2). The largest daily egg batches produced were 13, 11, and 7 eggs/female for corn earworm, beet armyworm-corn earworm, and beet armyworm females, respectively, by 20-, 22-, and 36-d-old females.

Daily progeny production was lower and delayed somewhat for females fed only beet armyworm compared with the other diets (Fig. 2). This resulted in a reduced r_m and ≈5-d delay in DT compared with corn earworm or beet armyworm-corn earworm females (Table 4). Although beet armyworm-corn earworm females produced fewer female progeny (R_0) than predators in the corn earworm treatment, females provided the beet armyworm-corn earworm diet had a higher peak of offspring production and shorter T, which directly affected the intrinsic rate of increase ($=\ln R_0/T$) (Table 4).

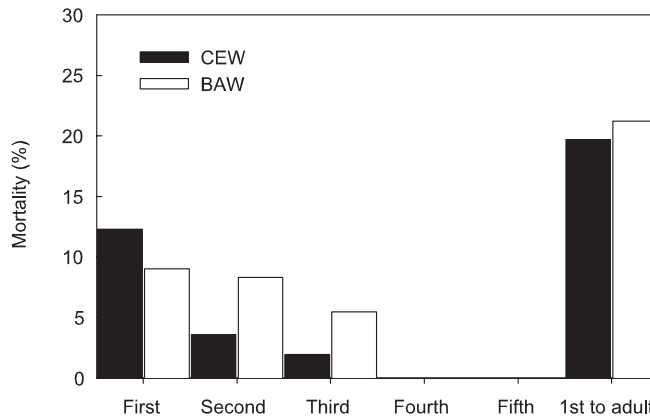


Fig. 1. Stage-specific mortality and total mortality from the first instar to adult emergence of *G. floridanus* fed *H. zea* eggs (corn earworm, CEW) and 1-d-old larvae of *S. exigua* (beet armyworm, BAW) ($n = 66$ nymphs for each prey; $26 \pm 1^\circ\text{C}$, L:D = 14:10).

The number of prey consumed per predator egg produced shows that females provided only beet armyworm consumed twice as many prey items per egg produced and were considerably less fecund than females that consumed corn earworm eggs ($df = 2, 38$; $F = 107.63$; $P < 0.0001$; Table 3). Prey species had a pronounced effect on both female survivorship and daily oviposition patterns (Fig. 2). Females fed only corn earworm eggs lived ≈ 20 d longer ($df = 2, 38$; $F = 9.87$; $P = 0.0003$) than those fed beet armyworm and beet armyworm-corn earworm (Table 3). Although females in the beet armyworm and beet armyworm-corn earworm treatments had similar longevity (Table 3), females provided only beet armyworm were less fecund and died between 28 and 78 d of adult life. In contrast, females in the beet armyworm-corn earworm treatment exhibited high survival and egg production initially, and lived between 44 and 65 d (Fig. 2). Egg production of females on the corn earworm diet also peaked relatively early, and longevity was increased from 51 to 110 d. Both the prolonged nymphal development and delayed age of first oviposition resulted in low r_m and λ , and extended population DT in females reared exclusively on beet armyworm. Despite their short reproductive period, female *G. floridanus* in the beet armyworm-corn earworm treatment produced a relatively high number of female progeny on a daily basis (Fig. 2).

Number of prey consumed over time varied between the prey items. The number of prey consumed per day by females in the corn earworm treatment increased after pairing, and was consistently high (≈ 15 eggs per day) 10–30 d after adult emergence; thereafter, predation declined with predator age (Fig. 3). However, predation of beet armyworm decreased slightly in the days subsequent to predator pairing, possibly because of the switch from using neonate beet armyworm larvae to 2-d-old beet armyworms that had fed on diet. Consumption of beet armyworm larvae by *G. floridanus* females was stable from 20 to 50 d after adult emergence, with ≈ 8 larvae consumed per day, and decreased sharply thereafter (Fig. 3).

G. floridanus nymphs, newly emerged virgin females, and paired females consumed 103, 50.7, and 728.7 corn earworm eggs, respectively, with an average of 882.4 prey consumed in the whole life. By comparison, when predators were reared with beet armyworm larvae, nymphal and newly emerged females (up to 3 d postemergence) consumed 129 and 45.8 beet armyworm neonates, respectively, and paired females consumed 446.3 of the 2-d-old beet armyworms, for a total of 621.1 beet armyworm larvae consumed throughout the predator's life (Tables 2 and 5). The effect of prey items on predation rate of adult males and females before mating was only marginally significant ($P = 0.0765$), but it was highly significant between genders within the same prey item ($P < 0.0001$), and there was a significant interaction between prey type and predator gender ($P = 0.0211$).

Adult Size. Size of *G. floridanus* was significantly affected by prey species (head: $df = 1, 60$; $F = 43.32$; $P < 0.0001$; thorax: $df = 1, 60$; $F = 69.54$; $P < 0.0001$) and predator gender (head: $df = 1, 60$; $F = 162.62$; $P < 0.0001$; thorax: $df = 1, 60$; $F = 236.42$; $P < 0.0001$) (Fig. 4). Females were larger than males when fed beet armyworm larvae (head: $t = 10.20$, $P < 0.0001$; thorax: $t = 8.66$, $P < 0.0001$) or corn earworm eggs (head: $t = 8.35$, $P < 0.0001$; thorax: $t = 12.50$, $P < 0.0001$) (Fig. 4). The thorax and head size values (length \times width) did not significantly correlate ($P > 0.05$) with any of the nymphal parameters (prey consumed and duration) or adult parameters (total number of eggs per female, longevity, and number of prey consumed) for predator females regardless of prey diet.

Discussion

The diet of nymphal and adult *G. floridanus* had considerable effects on various life-history traits of this predator. Despite being a polyphagous predator, there are obvious trade-offs in fitness related to the diet, as has been observed in other generalist predators (e.g., Evans et al. 1999, Mayntz and Toft 2001).

Table 2. Stage-specific predation (Mean \pm SE number consumed) from first instar to adult, and cumulatively for the nymphal period of males and females separately, of *G. floridanus* reared on corn earworm, *H. zea* eggs (corn earworm), and 1-day-old first instar larvae of *S. exigua* (beet armyworm) ($26 \pm 1^\circ\text{C}$, L:D = 14:10)

Prey	Nymphal stages					Female	Male	Gender effect
	1st instar	2nd instar	3rd instar	4th instar	5th instar			
Corn earworm n	3.8 \pm 0.19 57	7.0 \pm 0.38 55	12.0 \pm 0.63 54	22.0 \pm 0.63 53	45.1 \pm 2.65 53	103.0 \pm 1.84 24	100.2 \pm 1.70 29	$F_{1,51} = 1.40^{ns}$
Beet armyworm n	3.9 \pm 0.21 60	7.5 \pm 0.38 55	13.0 \pm 0.72 52	26.3 \pm 0.72 52	66.5 \pm 2.97 52	129.0 \pm 2.84 26	123.7 \pm 3.34 26	$F_{1,50} = 1.88^{ns}$
Statistics	$F_{1,115} = 0.0^{ns}$	$F_{1,108} = 0.13^{ns}$	$F_{1,104} = 0.3^{ns}$	$F_{1,103} = 6.11^{**}$	$F_{1,103} = 40.5^{***}$	$F_{1,48} = 174.2^{***}$	$F_{1,53} = 52.1^{***}$	

^{ns}P > 0.05, ^{**}P < 0.001, ^{***}P < 0.0001.

The preimaginal period of *G. floridanus* observed in the current study, although affected by prey species, fits within the range typical for other *Geocoris* spp. fed on lepidopteran eggs or larvae, depending on prey and temperature conditions. *Geocoris bullatus*, the closest relative of *G. floridanus*, developed from first instar to adult in ≈ 35 d when fed pea aphids and sunflower seeds at 24°C (Tamaki and Weeks 1972), which is considerably longer than the duration reported in this work for *G. floridanus*. Eubanks and Denno (2000) found that the pea aphid is poor quality prey, relative to corn earworm eggs, for *G. punctipes*; qualitative differences between pea aphids and lepidopteran eggs and larvae as prey may account for the discrepancy between our results and those of Tamaki and Weeks (1972).

The higher predation rate of *G. floridanus* nymphs on beet armyworm larvae relative to corn earworm eggs might be attributable to two properties of the prey. First, the young beet armyworm larvae are probably lower quality prey for *G. floridanus* than corn earworm eggs, and more beet armyworm larvae may need to be consumed to compensate for nutritional inadequacies. Second, mobility of prey may be an important stimulus for predatory behavior of big-eyed bugs. Eubanks and Denno (2000) found that although aphids are low-quality prey (compared with lepidopteran eggs) for *G. punctipes*, the predator preferred to attack aphids when given a choice between aphids and eggs, suggesting that active prey may be preferentially attacked. Large, ambulatory prey can cause mortality of nymphal big-eyed bugs through defensive activity (Crocker and Whitcomb 1980, Chiravathanapong and Pitre 1980). However, no defensive responses of beet armyworm neonates were observed when they were attacked in the current study. One avoidance mechanism used by the beet armyworms was to enter the piece of bean pod, obtaining shelter from the predator there. However, the number of prey provided was always excessive, so that there were always sufficient beet armyworms available outside of beans.

Although the fecundity of *G. floridanus* was affected by prey type, the fecundity observed in the current study fell within the range observed for other big-eyed bugs. Davis (1981) reported that *G. uliginosus*, *Geocoris lividipennis* Stål, *Geocoris pallens* (Say), and *G. punctipes* fed mealworm moth eggs produced from 96 to 347 eggs, with the lowest and highest fecundities found for *G. uliginosus* and *G. punctipes*, respectively, at 26.7°C . Hence, the r_m for these species ranged from 0.016 to 0.068 (Davis 1981), similar to those observed in this work for *G. floridanus*.

Fertility of eggs of *Geocoris* spp. in other laboratory studies is generally $\approx 70\%$, which is higher than fertility observed in this study for *G. floridanus*. This difference may be attributable to limited survival of males. Male longevity was significantly less than that of females (Table 3), and dead males in pairs were not replaced with live ones. The lack of mates later in life might have affected subsequent female fertility because of depletion of viable spermatozoa.

Table 3. Mean (\pm SE) reproductive characteristics of and prey consumption by *G. floridanus* fed *H. zea* eggs (corn earworm), 1st-instar *S. exigua* (beet armyworm) larvae (2-d-old, fed 1 day on artificial diet), and beet armyworm larvae as nymphs, and corn earworm eggs as adults (beet armyworm-corn earworm) ($26 \pm 1^\circ\text{C}$, L:D = 14:10)

Characteristics	Prey items ^a		
	Corn earworm (n = 19)	Beet armyworm (n = 16)	Beet armyworm-Corn earworm (n = 6)
Age at 1st oviposition ^b	5.0 \pm 0.23b	11.0 \pm 1.00a	5.5 \pm 0.22b
Egg incubation (days)	8.0 \pm 0.05a	8.1 \pm 0.06a	8.2 \pm 0.09a
No. of eggs per female	183.6 \pm 9.81a	56.6 \pm 3.97c	103.3 \pm 9.79b
Reproductive period (days)	59.7 \pm 2.11a	41.1 \pm 3.29b	39.2 \pm 3.27b
Eggs per day	3.1 \pm 0.18a	1.5 \pm 0.15b	2.7 \pm 0.25a
Fertility (hatching nymph)	0.56 \pm 0.06a	0.55 \pm 0.07a	0.54 \pm 0.05a
Female longevity (days)	71.2 \pm 3.15a	52.9 \pm 3.28b	53.8 \pm 3.64b
Male longevity (days)	36.7 \pm 3.68a	32.4 \pm 3.60a	37.5 \pm 3.78a
Prey item consumed/egg laid	4.1 \pm 0.18b	8.6 \pm 0.42a	-

^a Means followed by the same letter within rows do not differ significantly (Tukey HSD test; $P > 0.05$).

^b Time from adult emergence to initial oviposition.

The r_m refers to the immediate growth rate of a population under specified conditions only, and by itself provides a very limited glimpse into long-term population growth (Birch 1948). Hence, the use of r_m alone to compare treatment effects on populations is

not necessarily the most useful approach for assessing longer-term effects. The λ , which denotes the rate of population increase per unit of time, can be combined with longevity data to project population growth. Using the λ , it was apparent that *G. floridanus* population

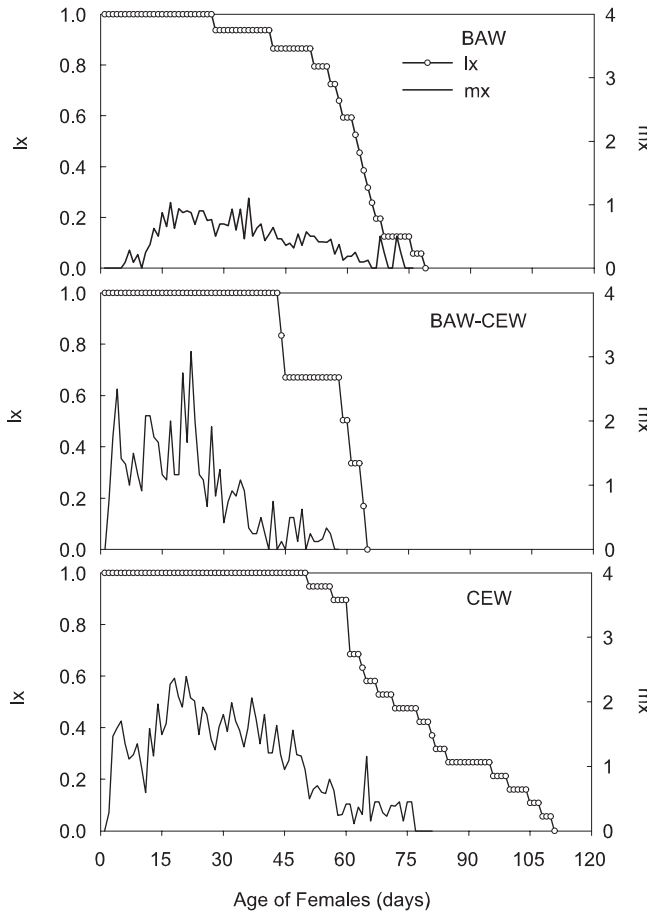


Fig. 2. Age-specific survivorship (l_x) and female offspring (m_x) of *G. floridanus* reared on: 1) 1-d-old beet armyworm (BAW) larvae throughout; 2) 1-d-old beet armyworm larvae as nymphs and adults fed corn earworm eggs (BAW-CEW); and 3) corn earworm eggs (CEW) ($26 \pm 1^\circ\text{C}$, L:D = 14:10).

Table 4. Life table parameters (mean \pm SE)^a of *G. floridanus* when fed *Helicoverpa zea* eggs (corn earworm), 1-d-old *S. exigua* larvae (beet armyworm), and when nymphs were fed beet armyworm larvae and adults fed corn earworm eggs (beet armyworm-corn earworm) (26 \pm 1°C, L:D = 14:10)

Prey items	R_o^b [(♀)(♀) ⁻¹]	T ^c (days)	r_m^d [(♀)(♀) ⁻¹ (day) ⁻¹]	λ^e	DT (days)
Corn earworm	37.7 \pm 1.99a	57.3 \pm 0.96a	0.062 \pm 0.0014a	1.064 \pm 0.0015a	11.2
Beet armyworm	11.5 \pm 0.77c	58.3 \pm 1.23a	0.041 \pm 0.0012b	1.042 \pm 0.0013b	16.9
Beet armyworm-corn earworm	21.9 \pm 1.98b	50.6 \pm 1.52b	0.060 \pm 0.0022a	1.062 \pm 0.0024a	11.5

^a Means within columns followed by the same letter do not differ significantly (Tukey's test; $P > 0.05$).

^b $R_o = \sum(l_x m_x)$; number of female eggs per female per generation, where l_x = the proportion of mated females alive at time x ; and m_x = age-specific fecundity multiplied by the respective sex ratio (0.45 and 0.5 sex ratio for corn earworm and beet armyworm).

^c $T = \sum(x l_x m_x) / \sum(l_x m_x)$; ^d $r_m = \ln R_o / T$; ^e $\lambda = e^{r_m}$.

growth was greatly limited when predator nymphs fed only on beet armyworm larvae, but that this limitation can be compensated for by consumption of more suitable prey (corn earworm eggs) in the adult stage.

Most of the variation in life-history attributes observed in this study are most likely attributable to qualitative differences in the prey. Prey scarcity was not a limiting factor, as the availability of prey always exceeded the predation rate. The life table parameters revealed that corn earworm eggs were better prey for *G. floridanus* than first-instar beet armyworms. Lepidopteran eggs have been demonstrated to be the best prey for big-eyed bugs (Cohen and Debolt 1983, Hennessee and Clayton 1985). Adult female *G. floridanus* consumed nearly 50% more corn earworm eggs than beet armyworm larvae, and produced $\approx 70\%$ more eggs. These numbers do not, however, indicate the potential for prey conversion: consumption of approximately twice as many beet armyworm larvae as corn earworm eggs was needed to produce one predator egg. Based on nutrient profiles of tobacco budworm eggs (*Heliothis virescens* F.; Cohen and Patana 1985), an artificial diet was developed for successfully rearing *G. punctipes* (Cohen 1985). However, even when the nymphal diet was less suitable, the availability of high-quality prey to adult *G. floridanus* allowed the pred-

ators to recover a significant portion of their reproductive potential. In the field, *G. floridanus* is most likely exposed to multiple prey items and probably has a mixed diet (including plant material) that may offset any reproductive drag imposed by constant ingestion of low-quality prey. However, the predators also have the ability to persist and reproduce when fed a constant diet of less suitable prey, such as neonate beet armyworms, which may have very important ramifications for the persistence of *G. floridanus* in the field.

G. floridanus can be characterized as a small species among the *Geocoris* spp. found in the Southeastern United States (see comparisons in Table 6). *G. floridanus* appears to be generally narrower than most other *Geocoris* spp., based on interocular distance and posterior width of the pronotum. A significant variation in adult size of *G. floridanus* resulted from prey type and predator gender (Fig. 4 and Table 6). There is often a direct relationship between a predaceous heteropteran's size and its fecundity and longevity, and at times the number of prey consumed. In an analysis of 57 oviparous species of different orders, Honek (1993) found that female size is a principal constraint on insect potential fecundity. In Heteroptera, for instance, nymphal development conditions have important effects on adult size and reproduction

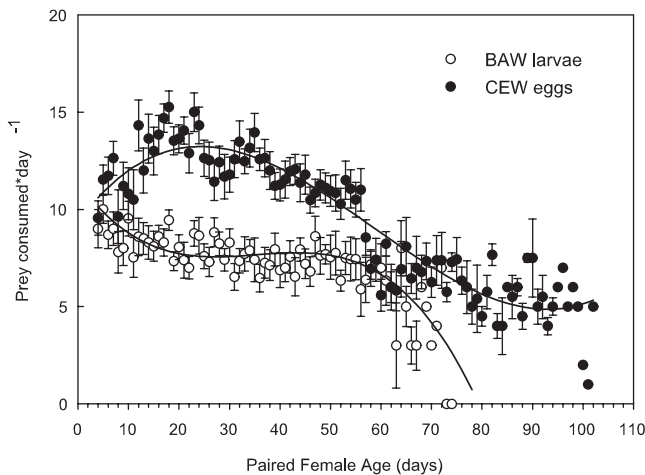


Fig. 3. Age-specific predation rate of *G. floridanus* females fed *H. zea* eggs (corn earworm, CEW) and 2-d-old first instar larvae of *S. exigua* (beet armyworm, BAW) (corn earworm eggs: $y = 9.349 + 0.350x - 0.00909x^2 + 0.0000517x^3$, $r^2 = 0.854$, $F = 185.52$, $P < 0.001$; and beet armyworm larvae: $y = 11.039 - 0.334x + 0.0103x^2 - 0.0001x^3$, $r^2 = 0.566$, $F = 26.45$, $P < 0.001$).

Table 5. Predation of *H. zea* (corn earworm) eggs and on 2-d-old *S. exigua* (beet armyworm) larvae by adult *Geocoris floridanus* ($26 \pm 1^\circ\text{C}$, L:D = 14:10)

Prey	Virgin adults ^a		Gender comparison	Mated females ^b
	♀	♂		♀
Corn earworm	50.7 ± 0.99	37.8 ± 1.28	$F_{1,49} = 55.43^{***}$	728.7 ± 24.38a
Beet armyworm	45.8 ± 1.01	37.4 ± 1.18	$F_{1,50} = 29.12^{***}$	446.3 ± 27.30b
Statistics	$F_{1,48} = 10.8^{**}$	$F_{1,53} = 1.05^{ns}$		$F_{1,34} = 60.14^{***}$

^{ns} $P > 0.05$, ^{**} $P < 0.001$, ^{***} $P < 0.0001$.

^a Fed beet armyworm larvae <24-h-old during the 3 days immediately following adult emergence (and prior to mating).

^b Fed 2-d-old beet armyworm larvae (fed 1 day on artificial diet) during adult lifespan.

(Evans 1982, O’Neil 1992), but reproduction is also largely determined by resources available to adults. Thus, the quality of food provided to beet armyworm-corn earworm females yielded reproductive output between that of beet armyworm and corn earworm females (Table 3). Although females in both diet treatments were roughly of the same adult size as a result of having the same nymphal diet (i.e., beet armyworm neonates) (Fig. 3), beet armyworm-corn earworm females exhibited higher reproductive output when

fed with a better prey (corn earworm eggs) after becoming adults.

Prolonged consumption of beet armyworm larvae yielded smaller predators than the other diets, and these smaller adults could conceivably be less fit than bugs reared on more suitable diets. However, in this study, no significant correlations were observed between female size (head and thorax sizes) and the number of prey consumed, or the fecundity and longevity of females within prey treatments. The lack of

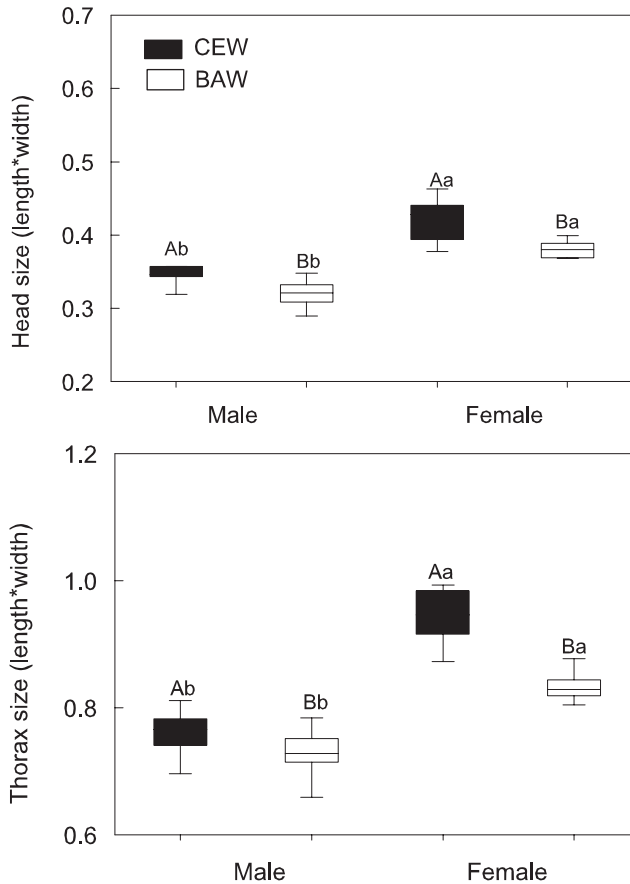


Fig. 4. Relationship of head and thorax (length × width) size of adult *G. floridanus* males and females reared on beet armyworm neonates (BAW) or corn earworm eggs (CEW) ($26 \pm 1^\circ\text{C}$, L:D = 14:10). Boxes under different upper case letters differ between prey within gender (full versus empty box), and boxes under different lower case letters differ between genders within prey treatments (empty versus empty, and full versus full boxes) by *t* test ($P = 0.05$).

Table 6. Adult body size (in mm) of *G. floridanus* ($26 \pm 1^\circ\text{C}$, L:D = 14:10) relative to other big-eyed bugs (data on other species from Davis (1981), (n = 10), who used eggs of *Sitotroga cerealella* Olivier as prey; temperature and photoperiod information not provided)

Prey for <i>G. floridanus</i> /Trait	<i>G. floridanus</i>		<i>G. punctipes</i>		<i>G. pallens</i>		<i>G. uliginosus</i>	
	♀ (n = 19)	♂ (n = 14)	♀	♂	♀	♂	♀	♂
Corn earworm								
Head length	0.57 ± 0.03	0.53 ± 0.01	0.57 ± 0.04	0.55 ± 0.03	0.47 ± 0.03	0.48 ± 0.04	0.46 ± 0.05	0.46 ± 0.05
Interocular distance	0.72 ± 0.02	0.64 ± 0.01	0.94 ± 0.02	0.84 ± 0.03	0.80 ± 0.04	0.73 ± 0.05	0.83 ± 0.03	0.77 ± 0.05
Pronotum length	0.74 ± 0.02	0.67 ± 0.02	0.99 ± 0.02	0.92 ± 0.02	0.77 ± 0.04	0.77 ± 0.05	0.81 ± 0.03	0.78 ± 0.02
Pronotum width	1.26 ± 0.02	1.13 ± 0.03	1.68 ± 0.05	1.52 ± 0.04	1.43 ± 0.06	1.28 ± 0.03	1.47 ± 0.04	1.37 ± 0.05
Beet armyworm								
(n = 16)		(n = 14)	—	—	—	—	—	—
Head length	0.56 ± 0.01	0.51 ± 0.02	NA	NA	NA	NA	NA	NA
Interocular distance	0.67 ± 0.01	0.63 ± 0.02	NA	NA	NA	NA	NA	NA
Pronotum length	0.71 ± 0.02	0.66 ± 0.02	NA	NA	NA	NA	NA	NA
Pronotum width	1.17 ± 0.02	1.10 ± 0.03	NA	NA	NA	NA	NA	NA

any significant correlation might be a result of the very limited variability in female size within prey treatments (Fig. 4), which may have been insufficient to produce a detectable relationship.

Based on our results, *G. floridanus* shares biological traits and predation potential with other big-eyed bug species (such as *G. punctipes*, *G. uliginosus*, and *G. pallens* Stål) considered of importance in crops across the United States, as cited by Sweet (2000). Our results also suggest that *G. floridanus* can survive and reproduce with less-than-optimal prey and can improve life-history traits when shifted to a more suitable prey item (e.g., lepidopteran eggs), yielding a numerical response close to that of females provided suitable prey throughout their lives. These findings are relevant to a multipest ecosystem, such as cotton or tobacco, in which various prey types of varying suitability are available. These results justify further studies of the biology and ecology of *G. floridanus*.

Acknowledgments

We thank Thomas J. Henry (Agricultural Research Service-United States Department of Agriculture, Smithsonian Natural History Museum, Washington, DC) and Merrill H. Sweet (Texas A&M University, College Station, TX) for their assistance during the process of the species identification, and for final identification. We also appreciate the helpful comments and suggestions of S. Kristine Braman (University of Georgia, Griffin, GA) and Merrill H. Sweet on an early version of this manuscript. This work was funded in part by the Georgia Cotton Commission and Cotton Incorporated. J.B.T. thanks the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) Foundation, Brazil (Grant BEX1315-005).

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Received 23 February 2004; accepted 12 May 2004.
