BIOLOGICAL AND MICROBIAL CONTROL

Functional Response of the Tiger Beetle *Megacephala carolina carolina* (Coleoptera: Carabidae) on Twolined Spittlebug (Hemiptera: Cercopidae) and Fall Armyworm (Lepidoptera: Noctuidae)

PUNYA NACHAPPA,[1] S. K. BRAMAN,[2] L. P. GUILLEBEAU, AND J. N. ALL

Department of Entomology, University of Georgia, Athens, GA 30602

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ABSTRACT The functional response of the tiger beetle *Megacephala carolina carolina* L. (Coleoptera: Carabidae) was determined on adult twolined spittlebug, *Prosapia bicincta* (Say) (Hemiptera: Cercopidae), and fourth instars of fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), in single-prey and two-prey systems. In the laboratory, *M. carolina carolina* demonstrated a type II functional response for *P. bicincta* and *S. frugiperda* in both single- and two-prey systems. Search efficiency of *M. carolina* declined for both prey as the initial number of prey increased. Of the total prey consumed, *M. carolina carolina* killed significantly more *S. frugiperda* than *P. bicincta* in the single-prey system (8.0 and 4.5, respectively) and the two-prey system (5.0 and 2.0, respectively). Estimates of attack coefficient, *a*, were not significantly different for *P. bicincta* and *S. frugiperda* in the single-prey (0.07 and 0.02) and two-prey systems (0.04 and 0.06), respectively. The handling time, T_h, was significantly greater for *P. bicincta* (5.02 and 10.64 h) than for *S. frugiperda* (2.66 and 4.41 h) in single- and two-prey systems, respectively. Estimations of attack coefficient and handling time in the single-prey system were used to predict prey preference of *M. carolina carolina*. No strong prey switching response was observed. *M. carolina carolina* showed no preference for either prey. However, in the presence of *S. frugiperda*, the functional response of the predator for *P. bicincta* was reduced. *M. carolina carolina* is a potential predator of one or more turfgrass pests and should be considered in conservation efforts.

KEY WORDS *Megacephala carolina carolina*, *Prosapia bicincta*, *Spodoptera frugiperda*, turfgrass, biological control

Managed landscapes have a diversity of plants and associated arthropod pests (Potter and Braman 1991, Vittum et al. 1999). Additionally, urban landscapes have a wealth of beneficial arthropods, including carabids (e.g., tiger beetles), staphylinids, mites, spiders, and ants (Reinert 1978; Cockfield and Potter 1983, 1984; Braman and Pendley 1993; Braman et al. 2000). These entomophagous invertebrates help limit pest outbreaks in urban landscapes (Reinert 1978, Cockfield and Potter 1984, Terry et al. 1993).

Prosapia bicincta (Say) (Hemiptera: Cercopidae), the twolined spittlebug, is an injurious and widespread pest of turfgrasses and ornamentals in southeastern United States (Beard 1973, Braman 1995, Vittum et al. 1999). Twolined spittlebug nymphs and adults are opportunistic xylem feeders and can feed on plants that provide fluids to meet their requirements (Pass and Reed 1965). There are few known natural enemies of twolined spittlebugs (Fagan and Kuitert 1969). *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), the fall armyworm, is a sporadic pest of turfgrasses especially in southeastern United States and Canada (Vittum et al. 1999). The larva is the injurious stage and has a variety of hosts, but it prefers grasses. The larvae feed on all aboveground plant parts (Cobb 1995).

The tiger beetle, *Megacephala carolina carolina* L. (Coleoptera: Carabidae), is a nocturnal predator found throughout southeastern United States (Graves and Pearson 1973, Pearson 1988). Tiger beetles have been captured in open areas, mud flats, lighted areas, shores of ponds, and woodland paths. Braman et al. (2002, 2003) reported *M. carolina carolina* collected in pitfall trap samples in turfgrasses and landscapes. *M. carolina carolina* has been shown to be a promising predator of *P. bicincta* adults (Nachappa et al. 2006).

Functional response relates change in predation rates to increasing prey density (Holling 1959). Functional response can be used to determine whether a predator is able to regulate the density of its prey when

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[1] Current address: Department of Entomology, Kansas State University, 123 West Waters Hall, Manhattan, KS 66506–4004.

[2] Corresponding author, e-mail: kbraman@griffin.uga.edu.

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the response depends on density (Murdoch and Oaten 1975). By their shape Holling (1959) described three predator functional responses in which the number of prey consumed rises linearly, hyperbolically, or sigmoidally, for a type I, type II, and type III response, respectively. Most invertebrate predators demonstrate type II response, whereas the type III is exhibited by both vertebrate and invertebrate predators (Riechert and Lockley 1984).

The effects of alternative prey on the population dynamics of target prey and predator have focused on functional and numerical responses (Eubanks and Denno 2000). The primary effect of alternative prey on the functional response is the decrease in the consumption of the target prey due to prey switching or saturation (Murdoch 1969). However, the target prey also can have a positive effect on biological control by increasing the predator's numerical response (Settle et al. 1996).

In summary, the ability of a predator to control a prey population is dependent on the predator functional and numerical response. However, these responses are influenced by several factors, including the density-dependent behavioral patterns, developmental response, prey preference, use of alternative prey, and predator's interaction with other predators. Still, scientists involved in biological control programs determine the potential of a natural enemy by using functional response studies with an individual predator/parasitoid feeding on a single patch of prey species (Flinn et al. 1985, De Clercq et al. 1998, Wells and McPherson 1999, Lester et al. 2000, Lester and Harmsen 2002, Stewart et al. 2002). In our study, the functional response, handling time, and attack coefficient of *M. carolina carolina* on *P. bicincta* adults and fourth instar *S. frugiperda* larvae were determined when prey items were offered alone (single-prey) or simultaneously (two-prey system) in the same arena. We chose these two prey types because of their obvious morphological differences which might affect the functional response parameters (attack coefficient and handling time) and prey preference. Moreover, both insects and the predator inhabit turfgrass and landscapes as their common habitat.

Materials and Methods

Insect Source. Adult tiger beetles were collected from pitfall traps inserted in centipedegrass, *Eremochloa ophiuroides* (Munro) Hack. and fescue, *Festuca arundinaceae* Schreb, plots in Griffin, GA. Beetles were maintained in 10-cm-diameter petri dishes at room temperature and a photoperiod of 14:10 (L:D) h, and they were fed varying prey items such as field crickets, *Gryllus rubens* Scudder, as food. *P. bicincta* adults were field-collected from local residential areas and commercial landscapes from June to September around Griffin. Spittlebugs were maintained using procedures described by Shortman et al. (2002). Adults were maintained on centipedegrass in 800-ml mason jars ventilated with 32-mesh screen. The jars were then placed in environmental chambers (Conviron, Manitoba, Canada) and maintained at 24°C, 75–80% RH, and a photoperiod of 15:9 (L:D) h. Adult *P. bicincta* were used for the experiments.

Fourth instars of *S. frugiperda* were obtained from a laboratory-reared colony. *S. frugiperda* eggs were obtained from USDA–ARS Crop protection and Management Research Unit in Tifton, GA. Neonate fall armyworms were maintained on commercial diet (Bio-Serve, Frenchtown, NJ) in 32-ml diet cups, and placed in environmental chambers (Percival Scientific, Perry, IA) at 24°C, 75–80% RH, and a photoperiod of 15:9 (L:D) h. Fourth instars of *S. frugiperda* larvae were used for experiments.

Experimental Design. All experiments were conducted at room temperature (24 ± 1°C) under fluorescent light set at a light cycle of 14:10 (L:D) h, and relative humidity was maintained at 70%. Experimental arenas consisted of 18.0- by 8.0-cm plastic cages (Pioneer Plastics, Dixon, KY), with 254.34-cm^2 total surface area. Centipedegrass (13.2 g) was provided in the cage to simulate a more natural situation and thus produce a functional response curve that is more field applicable. Tiger beetles were held without food for 4 d before placing in the cage with prey. Preliminary studies showed that *M. carolina carolina* prey consumption was maximum 4 d after starvation. One, 3, 5, 7, and 11 adult *P. bicincta* were placed in a cage with a single tiger beetle. Fourth instars of *S. frugiperda* larvae were placed in a cage with a single tiger beetle at similar prey densities (1, 3, 5, 7, and 11) and addition of prey densities nine and 15. There were 10 replicates for both *P. bicincta* and *S. frugiperda* at each prey density. Controls were maintained for both prey species separately without the predator. The experiment was conducted simultaneously for both *P. bicincta* and *S. frugiperda* as prey at each prey density. After 24 h, the predator was removed from the cage, and the number of live prey was determined.

Prey Preference. To determine the predator functional response in the presence of two prey types, both *P. bicincta* adults and fourth instars of *S. frugiperda* were placed with a single predator in a plastic cage. Prey preference experiments were conducted under the same conditions as those described above. Tests were conducted using one, three, five, and seven adult *P. bicincta* and similar numbers of fourth instars of *S. frugiperda* in each cage; hence, a total of two, six, 10, and 14 of both prey types per plastic cage. The experiment had 10 replicates at each prey density and was conducted simultaneously for all replicates. Controls had no predator present.

Statistical Analysis. Data on the prey killed at each prey density in single- and two-prey systems were analyzed using PROC GLM procedure (SAS Institute 2001). The most effective way to distinguish type of functional response involves performing a logistic regression of the proportion of prey killed related to their initial number present (Trexler et al. 1988). The linear coefficient of the plot of the proportion of prey killed in relation to the initial prey density is negative for type II response and positive for type III response (Juliano 1993). Data on the proportion of prey killed

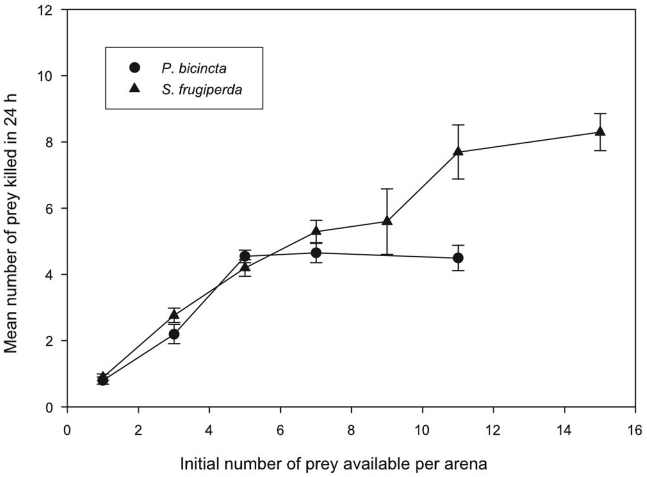

Fig. 1. Mean ± SE number of adult *P. bicincta* and fourth instars of *S. frugiperda* killed by *M. carolina carolina* in single-prey system.

versus initial prey number present were fitted to cubic, quadratic, and linear models and compared with the expected values predicted by the "random-predator" equation (Rogers 1972) by using Maximum likelihood analysis of PROC CATMOD of SAS (SAS Institute 2001). The type II functional response was modeled using the random-predator equation of Rogers (1972)

$$N_e = N\{1 - \exp\,[\mathrm{a}\,(T_h\,N_e - T)\,]\}$$

where N_e is number of prey killed, *N* is number of prey available (initial number of prey), *a* is attack coefficient, T_h is handling time, and *T* is total time prey is exposed to the predator.

The parameters of the functional response, *a*, and $T_{h,}$ were calculated using Gauss–Newton estimate method as performed by PROC NLIN of SAS, and a Student's *t*-test was used to determine significant differences (SAS Institute 2001). Several methods of nonlinear fittings are available. Because functional response data sets usually show heteroscedasticity, we chose to maximize a Gaussian likelihood instead of least-square procedure (Juliano and Williams 1987).

The estimates of *a* and T_h computed for individual prey can be used in a mathematical model to describe the predation rate when both prey items are presented simultaneously under the null hypothesis that there was no preference between them (Cock 1978). The model is as follows:

$$N_{ep}/N_{es} \;=\; 1 - \exp\,(a_p\,T_s)\;N_p/1 - \exp\,(a_s\,T_s)\;N_s$$
$$=\; \gamma\;N_p/N_s$$

where γ is prey preference; the variables are the same as previous equation, except the subscripts *p* and *s* indicate *P. bicincta* and *S. frugiperda*, respectively; and T_s = the time available for searching is given by $(T_{hp}\,N_{ep} - T) - (T_{hs}\,N_{es} - T)$.

Prey preference is defined as the disproportionate selection of one type of prey, relative to the proportion of prey available in the environment (Flinn et al. 1985). Prey preference is dependent on number of prey eaten, handling time, and the total time available in addition to search efficiencies. The prey preference term (γ) cannot be estimated directly from the equation, but the equation can be used to predict actual consumption of prey and hence the ratio of N_{ep}/N_{es} when both prey are present simultaneously (Cock 1978). A chi-square test was used to determine statistical difference between experimental results and model predictions (SAS Institute 2001).

Results and Discussion

Prey Killed and Search Efficiency. Results of this study confirm previous reports that tiger beetles are voracious predators of various living arthropods (Pearson 1988). To our knowledge, this is the first published report of functional response of *M. carolina carolina* to two of its prey, *S. fruigperda* and *P. bicincta.* Comparisons of proportion of prey killed at each density show that *M. carolina carolina* caused significant mortality of both *S. fruigperda* and *P. bicincta* in a single-prey system ($F = 4.2$, df = 1, $P < 0.04$) and a two-prey system ($F = 30.34$, df = 1, $P < 0.0001$). *M. carolina carolina* killed between 0.9 and 8.3 *S. fruigperda* fourth instars with ≈8.5 at the upper asymptote (Fig. 1). *M. carolina carolina* killed between 0.85 and 4.65 *P. bicincta* adults with ≈5.0 at the upper asymptote (Fig. 1). Predators that demonstrate functional response curves with a high asymptotic value are considered to have a strong functional response, i.e., they kill more prey than needed to complete development. Based on our results, *M. carolina carolina* shows a much stronger functional response to *S. frugiperda* than *P. bicincta* (Fig. 1). Control mortality was insignificant with 95% survival ($n = 90$) of *P. bicincta* and 100% ($n = 110$) survival of *S. frugiperda* larvae after 24 h when prey were offered alone without *M. carolina*

Table 1. Procedure CATMOD analysis of max likelihood estimates ± SE form logistic regression of the proportion of prey killed by *M. carolina carolina* as a function of initial prey density

Prey type	Linear parameter (N0)				Quadratic parameter (N02)				Cubic parameter (N03)			
	Estimate ± SE	χ^2	df	*P*	Estimate ± SE	χ^2	df	*P*	Estimate ± SE	χ^2	df	*P*
Single-prey system												
P. bicincta	−0.03 ± 0.01	−3.61	1	0.0007	0.17 ± 0.35	0.23	1	0.62	−0.01 ± 0.01	0.28	1	0.59
S. frugiperda	−0.02 ± 0.01	−3.85	1	0.0003	0.01 ± 0.02	0.41	1	0.52	−0.04 ± 0.03	0.10	1	0.75
Two-prey system												
P. bicincta	−0.05 ± 0.02	−2.15	1	0.03	0.31 ± 0.42	0.32	1	0.45	−0.02 ± 0.03	0.74	1	0.38
S. frugiperda	−0.04 ± 0.01	−3.68	1	0.0007	0.38 ± 0.28	0.40	1	0.58	−0.03 ± 0.01	0.56	1	0.45

carolina. There was 100% survival in controls, with both prey items together without the predator.

Search efficiency is measured by the proportion of prey killed at each density. In the single-prey system, the proportion of *S. frugiperda* and *P. bicincta* prey killed decreased as the initial prey density increased. Food is one of the limiting resources for tiger beetles; the rate of food intake affects size of larvae, adults that in turn affects fecundity (Pearson and Knisley 1985). Tiger beetles locate immobile or dead prey tactilely and moving prey visually. In prey-poor habitats, tiger beetles spend most of their time searching for scarce prey items, whereas in prey-rich habitats their search efficiency is nearly zero, because they encounter prey easily (Pearson and Knisley 1985). Search efficiency declines at a certain point as the predator is capable of capturing and handling only a finite number of prey in a given amount of time (O'Neil 1997).

Predator Functional Response. Most insects exhibit a type II functional response under laboratory conditions, which is similar to the results of our study. In the single-prey system, the best fit for *P. bicincta* functional response data was linear; the linear coefficient ± SE of the proportion of *P. bicincta* killed versus initial number of prey was negative, and the quadratic coefficient was positive, indicating a type II functional response (Table 1). Additionally, the shape of the curve of proportion of *P. bicincta* killed versus initial number of prey indicates the type of functional response (Trexler et al. 1988, Wells and McPherson 1999). A negative slope along all parts of the curve indicates a type II response. The slope of the proportion of *P. bicincta* adults killed is negative along all parts, suggesting a type II functional response (Fig. 2). The random predator model fit the observed data well for *P. bicincta* with a raw r^2 of 0.93.

In the single-prey system, the best fit for *S. frugiperda* functional response data was also linear; the linear coefficient ± SE of the functional response was negative, and the quadratic coefficient was positive, indicating a type II functional response (Table 1). The slope of proportion *S. frugiperda* killed was also negative along all parts of the curve, indicating a type II response (Fig. 2). The random predator model fit the observed data similarly for *S. frugiperda* with a raw r^2 of 0.91.

In the two-prey system, the best fit for *P. bicincta* and *S. frugiperda* functional response data was linear; the linear coefficient ± SE of the proportion of *P. bicincta* killed versus initial number of prey was negative, and the quadratic coefficient was positive, indicating a type II functional response (Table 1). Results of both *P. bicincta* and *S. frugiperda* in the two-prey system indicated that the predation rate decreases as predator satiation reaches an upper limit of food consumption. The slope of the curve for *P.*

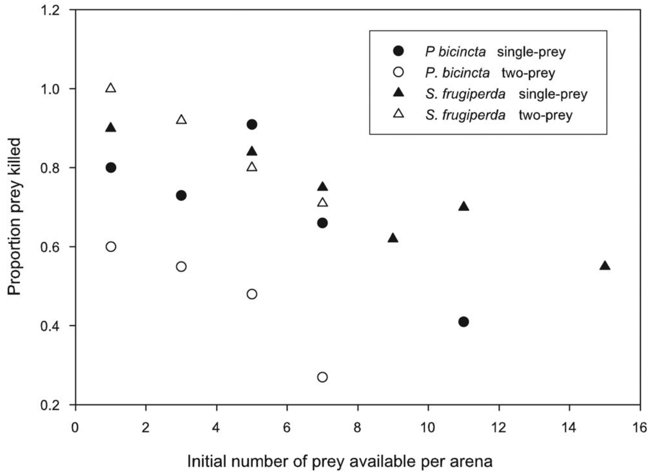

Fig. 2. Proportion of adult *P. bicincta* and fourth instars of *S. frugiperda* killed by *M. carolina carolina* in both prey systems.

Table 2. Random predator model estimates of attack coefficients (*a*) and handling time (T_h) of *M. carolina carolina* when challenged with *P. bicincta* adults and *S. frugiperda* fourth instars in single- and two-prey systems

Prey type	*n*	*a*		T_h (h)	
		Coefficient ± SE	95% CI	Coefficient ± SE	95% CI
Single-prey system					
P. bicincta	50	0.07 ± 0.03a	0.007–0.14	5.02 ± 0.29b	4.42–5.62
S. frugiperda	69	0.02 ± 0.06a	0.009–0.03	2.66 ± 0.22a	2.21–3.11
Two-prey system					
P. bicincta	39	0.04 ± 0.03a	0.033–0.11	10.64 ± 1.74b	7.10–14.19
S. frugiperda	39	0.06 ± 0.03a	0.01–0.14	4.41 ± 0.53a	3.32–5.49

Means in each column followed by the same letter are not significantly different ($P > 0.05$).

bicincta and *S. frugiperda* together and total prey consumed was negative, which further supports the conclusion that *M. carolina carolina* exhibits a type II functional response two-prey system (Fig. 2). The random predator model fit the data reasonably well for *P. bicincta* type II response in the two-prey system with a raw r^2 of 0.71. The model fit the data for *S. frugiperda* much better with a raw r^2 of 0.91.

Parameters of the Functional Response. Functional response parameters *a* and T_h were estimated using random predator model (Rogers 1972). The *a* and T_h values are important to determine the patterns and strategies of predators. The estimates of attack coefficients were not statistically different for *P. bicincta* and *S. frugiperda* in single- and two-prey systems (Table 2). Handling time is a combined effect of capture and consumption of prey, and it varies according to the prey type (Faria et al. 2004). Some prey are easily found and captured, which is directly correlated to decrease in time and energy spent by the predator (De Clercq et al. 1998). The handling time for *P. bicincta* was 5.02 h and *S. frugiperda* 2.66 h in the single-prey system. In the two-prey system, handling time increased to 10.64 and 4.41 h, respectively, for *P. bicincta* and *S. frugiperda.* The handling time for *P. bicincta* was significantly greater ($P < 0.05$) than for *S. frugiperda* in both single- and two-prey systems (Table 2). It has been shown that handling time is proportional to the size of the prey: the larger the prey longer the time taken to eat it (Flinn et al. 1985). *P. bicincta* might represent a poor prey compared with fall armyworm, because the former weighed significantly less than *S. frugiperda.* The average weight of 10 *P. bicincta* was 0.33 g compared with 2.07 g for same number of *S. frugiperda.* The variability observed in the handling time indicates a reverse result, which could be due to the defense or escape response of the prey (Pastorok 1981).

Prey Preference. We compared the observed and estimated number of prey eaten under the null hypothesis that *M. carolina carolina* shows no preference for either prey, *P. bicincta* and *S. frugiperda.* There was no significant difference between estimated and observed number of prey killed for *P. bicincta* ($\chi^2 = 0.60$, df = 3, $P = 0.89$) and *S. frugiperda* ($\chi^2 = 0.67$, df = 3, $P = 0.87$), which indicates no preference for either prey (Fig. 3). However, in the presence of *S. frugiperda* we observed significant reduction in the functional response to *P. bicincta* ($P < 0.0001$). Results strongly suggest change in the searching behavior of *M. carolina carolina* when both prey items were offered together. *M. carolina carolina* continued to kill *P. bicincta* even in the presence of *S. frugiperda,* which is an interesting result. No strong switching behavior was noticed, where at higher prey densities one prey species is not consumed due to the predator's prefer-

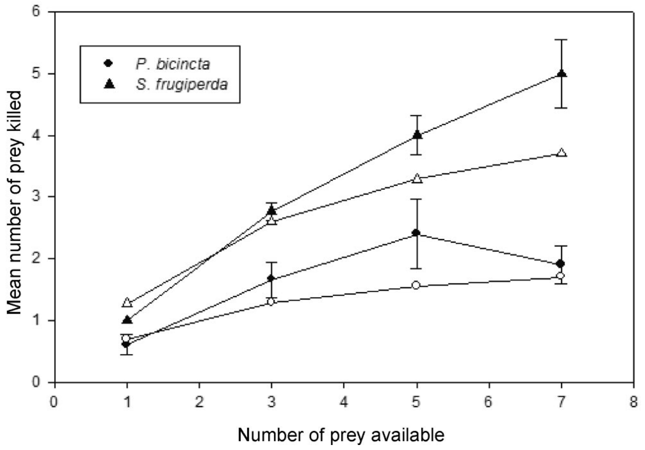

Fig. 3. Functional response of *M. carolina carolina* to *P. bicincta* and *S. frugiperda* in a two-prey system. Closed symbols indicate observed data and open symbols indicate expected means.

ence for another prey species (Flinn et al. 1985). The functional response for *P. bicincta* seems to exhibit a plateau in terms of saturation much earlier than *S. frugiperda* may be due to the fact that the predator spent more time consuming *S. frugiperda.* Another explanation for the different saturation responses of both prey may be attributed to the differential handling time (Faria et al. 2004). Although we did not detect any strong preference for either prey item, differences in consumption of the two turfgrass pests provide information concerning its capacity to control these two pests in their common habitat.

Our results indicate that *M. carolina carolina* demonstrates a type **II** functional response to both prey species. The only difference observed was a much stronger functional response to *S. frugiperda* (higher asymptote) than *P. bicincta.* The total response of a predator includes the functional and numerical responses, dispersal rate; predator interference and a development response (Price 1997). We only examined functional response; however, similar studies have not been done for *M. carolina carolina* or other tiger beetles. Given the taxonomic diversity of the group even in southeastern United States, and the range of habitats its members exploit, there is a need to acquire new information about biology and ecology of tiger beetles. Our study provides evidence suggesting the potential importance of tiger beetles in suppressing common turfgrass pests.

There is a paucity of information about the economic potential of tiger beetles in controlling crop pests (Pearson 1988). Generalist predators, such as tiger beetles, feed on a variety of prey, allowing them to survive when the target prey is scarce. Previous reports have shown that tiger beetles reduce insect populations in many agroecosystems (Sastry and Appanna 1958). *Megacephala virginica* L., a tiger beetle common in southeastern United States, has been shown to be a predator of mole crickets (*Scapteriscus* spp.) in turf and pasture (Pearson 1988). In such systems, an examination of predation on multiple prey species is important, especially when examining a potential biological control agent. Although we did not observe any strong prey switching response in the two-prey systems, in the presence of *S. frugiperda* the functional response of predator toward *P. bicincta* was reduced. However, the effects of alternative prey on predation are complex and could be specific to prey stage, prey species, and predator.

In conclusion, the functional response and the effects of alternate prey of *M. carolina carolina* may alone be of little predictive value in determining effectiveness of the predator in a biological control program. However, the responses do indicate that *M. carolina carolina* will consume both prey species. Our study was conducted in laboratory bioassays with single-prey and two-prey systems, which may not allow for predictions about the effectiveness of *M. carolina carolina* for augmentative biocontrol in a realistic habitat. Field studies that incorporate variables such as host plant resources, multiple prey and predators, cannibalism are necessary to further determine potential of *M. carolina carolina* in the field. However, artificial arenas are appropriate for simple comparisons of the physiological capacities of the predator to various preys. Nevertheless, the functional responses of *M. carolina carolina* both prey species serve as a useful guideline for estimating the potential impact of the predator on *P. bicincta* and *S. frugiperda* populations. *M. carolina carolina* is a valuable ubiquitous predator and should be a target of conservation efforts.

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