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ABSTRACT *Coccinella septempunctata* L. and *Harmonia axyridis* Pallas are key natural enemies of soybean aphid, *Aphis glycines* Matsumura, in North America. Third instars, adult females, and adult males of both *C. septempunctata* and *H. axyridis* exhibited a type II functional response for predation toward adult soybean aphids at $26 \pm 1°C$. In *C. septempunctata*, the functional response curve of adult males differed from those of third instars and adult females, but there was no difference between third instars and adult females. In *H. axyridis*, the functional response curves of larvae, adult females, and adult males all differed significantly. Third instars and adult females consumed significantly more soybean aphids than did adult males at prey densities of 150 and 180 aphids per arena for *C. septempunctata* and at prey densities of 60, 90, 120, 150, and 180 aphids per arena for *H. axyridis*. The theoretical maximum daily predation rate of adult aphids by *C. septempunctata* was predicted to be 204 per third instar, 277 per adult female, and 166 per adult male, and 244, 156, and 73, respectively, for *H. axyridis*. Third instars and adult females of both species consumed significantly more aphids than did adult males on soybean plants with the recommended action threshold of 250 soybean aphids per plant. Both *C. septempunctata* and *H. axyridis* have high predation capacities and are important in suppressing soybean aphid populations.

KEY WORDS functional response, biological control, seven-spotted lady beetle, multicolored Asian lady beetle, soybean aphid

Soybean aphid, *Aphis glycines* Matsumura (Homoptera: Aphididae), is native to Asia and has become a severe pest of soybean, *Glycine max* (L.) Merrill, since its discovery in North America in 2000 (Rutledge 2004, Venette and Ragsdale 2004). Natural enemies are important to the regulation of soybean aphid populations in Asia (Quimio and Calilung 1993, Chang et al. 1994, van den Berg et al. 1997, Heimpel et al. 2004, Liu et al. 2004, Wu et al. 2004, Miao et al. 2007) and in North America (Fox et al. 2004, 2005; Rutledge et al. 2004; Rutledge and O'Neil 2005; Costamagna and Landis 2006, 2007; Costamagna et al. 2007). In North America, predators commonly dominate the natural enemy community (Rutledge et al. 2004, Costamagna and Landis 2007). Generalist predators such as the seven-spotted lady beetle, *Coccinella septempunctata* L., and the multicolored Asian lady beetle, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), account for most of the observed mortality and are very effective at reducing aphid numbers on a per capita basis (Costamagna and Landis 2007).

The current action threshold of 250 soybean aphids per plant (NCSRP 2006, Baute 2007) was validated by determination of an economic threshold of 273 aphids per plant (Ragsdale et al. 2007); although natural enemies would have been present in study fields, natural enemy numbers were not explicitly taken into account in development of either threshold. To incorporate predator effects into the action threshold, it is necessary to determine the functional response for each predator species. Functional response is defined as the relationship between the number of prey consumed per predator and the prey density (Solomon 1949) and is a valuable tool for assessing the potential impact of a natural enemy on pest population growth and predicting the potential for success of biological control agents (Hassell 1978, Houck and Strauss 1985, Tully et al. 2005). Holling (1959a) categorized functional responses into three basic types. The type I response is characterized by a linear rise with a constant attack rate over all prey densities until satiation is reached. In the type II response, the attack rate decreases as prey density increases. Type III is represented by a sigmoid curve where the attack rate increases with increasing prey density and decreases toward satiation. Most studies are confined to type II and III responses because these are the most commonly observed in nature (Juliano 2001).

Many studies have been conducted on the functional responses of *C. septempunctata* and *H. axyridis* to aphids, including the pea aphid, *Acyrthosiphon pisum* (Harris) (Carter et al. 1984), *Aphis citricola* van der Goot (Wang et al. 1999, Chen et al. 2005), cotton

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aphid, *Aphis gossypii* Glover (Xia et al. 2003, Lee and Kang 2004), *Aphis robiniae* Macchiati (Wang et al. 1999), *Chaitophorus populeti* (Panzer) (Zhang and Liu 2006), *Hyalopterus amygdali* (Blanchard) (Zhang et al. 2004), turnip aphid, *Lipaphis erysimi* (Kaltenbach) (Sinha et al. 1982, Xue et al. 1996, Kumar et al. 1999, Omkar and Srivastava 2003, Zhang and Liu 2006), tobacco aphid, *Myzus nicotianae* (Blackman) (Liu et al. 2002), green peach aphid, *Myzus persicae* (Sulzer) (Xue et al. 1996, Ma et al. 2000, Hou and Wan 2004, Hao and Hao 2005), waterlily aphid, *Rhopalosiphum nymphaeae* L. (Ge et al. 2006), bird cherry-oat aphid, *Rhopalosiphum padi* L. (Lou 1987, Zhang and Liu 2006), greenbug, *Schizaphis graminum* (Rondani) (Hu 1992), English grain aphid, *Sitobion avenae* (F.) (Skirvin et al. 1997), and yellow clover aphid, *Therioaphis trifolii* (Monell) (Zhang et al. 2007). However, the functional responses of *C. septempunctata* and *H. axyridis* to the soybean aphid have not been described. Xue et al. (1996) reported that the predation capacity of *C. septempunctata* on *M. persicae* was greater than on *L. erysimi*, which might be caused by the physical structures and wax on the body of *L. erysimi.* These results suggest that predation data collected from other aphid species may not apply to the soybean aphid, although studies with very similar species such as cotton aphid may be more useful.

The purpose of this study was to better understand the interaction between these two generalist predators and soybean aphids and their potential to suppress soybean aphid populations by determining the functional responses of third instars, adult females, and adult males to soybean aphids. We also examined predation by these species on aphids on soybean plants at the current action threshold of 250 aphids per plant under laboratory conditions.

Materials and Methods

Insect Culture. Soybean aphids were collected from a soybean field near Guelph, Ontario, Canada. Aphids were reared on soybean cultivar Colby in a growth room held at $24 \pm 2°C$ and 16:8 L:D with fluorescent bulbs (Cool White; Sylvania, Mississauga, Ontario, Canada). Soybean seeds were soaked in Cell-Tech Soybean *Bradyrhizobium japonicum* inoculant (EMD Crop Bioscience Canada, Belgrave, Ontario, Canada) before planting and were watered using 20–20-20 fertilizer water *ad libitum.*

Adult beetles were obtained from 10 soybean fields in Kent and Lambton counties, Ontario, Canada, where soybean aphid populations were present. Beetles were held in 10 by 20 by 25-cm nylon mesh cages in a growth room at $24 \pm 2°C$ and 16:8 L:D and fed a mixed diet of both soybean aphid reared on soybean (as above) and bird cherry-oat aphid. Bird cherry-oat aphid starter colonies (Aphid Banker System; Plant Products, Brampton, Ontario, Canada) were reared on barley grown in 14 cm diameter by 14 cm high pots and held within a large mesh enclosure in a greenhouse at $23 \pm 3°C$ and 16:8 L:D. Even-age cohorts of lady beetles from eggs laid on the same day were reared in separate cages, with new aphid-infested plants introduced twice weekly. All beetle eggs found in adult cages were moved to separate cages and given a fresh supply of aphids.

Functional Responses. To examine the functional response of third instar, adult female and adult male lady beetles, V1 soybean plants, 15–18 cm high with two fully expanded unifoliates, were each cut above the cotyledon. Stems of individual excised plants were inserted through holes in the lids of bottles containing 20 ml water. Adult soybean aphids selected on the basis of body size were transferred to these plants at densities of 30, 60, 90, 120, 150, and 180 per plant. Each plant unit was placed in a clear plastic container (10 cm diameter by 8 cm height; Shortreed Paper, Guelph, Ontario, Canada). Mesh-covered holes in the lid provided ventilation. Predation of first instars produced during the experimental period was ignored because of the small biomass this life stage represented.

A single newly molted third instar or a 1- to 3-wk-old adult lady beetle was introduced into each arena. Newly molted third instars were obtained by collecting second instars, which had ceased feeding and were preparing to molt, from the stock colony and holding them individually in small containers without food. After 24 h, newly molted third instars were selected for experimentation. Adults were starved for 24 h before being introduced to arenas. Arenas were kept in a controlled environment chamber at $26 \pm 1°C$ and a 16:8-h L:D period. After 24 h, the number of prey consumed was recorded. Each aphid density was replicated 10 times. In addition, controls for each aphid density were conducted without predators to control for other sources of aphid mortality and replicated three times.

Predation on Soybean Plants. To examine predation of aphids on whole plants, 250 aphid adults were transferred with a paintbrush to V3 soybean plants with three unfolded trifoliates. Each plant was held in a plastic cage (9 cm diameter by 30 cm high) with a mesh top to provide ventilation. A single third instar, adult female, or adult male lady beetle was introduced into each cage. Cages were kept in a controlled environment chamber, as above, and after 24 h, the number of prey consumed was recorded. The experiment was replicated 12 times for the larval stage of *C. septempunctata* and 10 times each for the larval stage of *H. axyridis* and adults of both species. Predation of first instars produced during the experimental period was ignored because of the small biomass this life stage represented. Three replications of aphids in the absence of predators were conducted as controls.

Statistical Analyses. Functional responses were described using two-stage analysis (Juliano 2001). A cubic logistic regression (equation 1) between proportion of prey consumed and initial prey density was first performed to determine the type of functional response curve (Juliano 2001):

$$\frac{N_a}{N_0} = \frac{\exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)}{1 + \exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)} \quad [1]$$

where N_a is the number of prey consumed, N_0 is the initial prey density, and P_0, P_1, P_2, and P_3 are the intercept, linear, quadratic, and cubic coefficients, respectively. If the linear coefficient, P_1, is significantly negative, the predator is displaying a type II functional response; if positive, there is a type III functional response (Juliano 2001). If a cubic equation yields a nonsignificant cubic coefficient, it is desirable to reduce the model by eliminating the cubic coefficient from equation 1 and to retest the other parameters (Juliano 2001).

Because the logistic regression analysis indicated that our data fit type II in each case, further analyses were restricted to the type II functional response. The Holling's disc (equation 2) (Holling 1959b) and the random predator (equation 3) (Royama 1971, Rogers 1972) were used to model the relationship between the number of prey consumed (N_a) and initial prey density (N_0):

Holling's disc equation:

$$N_a = \frac{aN_0}{1 + aT_hN_0} \qquad [2]$$

Random predator equation:

$$N_a = N_0[1 - \exp(aT_hN_a - a)] \qquad [3]$$

where a is the instantaneous searching rate and T_h is the handling time per prey item. A nonlinear regression procedure (NLR) based on the Levenberg-Marquardt method (SPSS 2006) was performed to estimate the parameters a and T_h. The starting values of a and T_h required by the NLR procedure were found by linearly regressing $1/N_a$ against $1/N_0$. The resultant y-intercept is the initial estimate of T_h and the reciprocal of the regression coefficient (slope) is an estimate of a (Livdahl and Stiven 1983, Watson et al. 2000). These initial estimates were refined by NLR. Data did not fit the model if the asymptotic 95% confidence intervals (CIs) of a and T_h estimates included zero (i.e., the estimates did not differ significantly from zero) (Watson et al. 2000, SPSS 2006). If the data fit both models, the best model was selected based on the value of the coefficient of determination (R^2).

Differences between the functional response curves in different stages and sexes of lady beetles (referred to as "stages" throughout for simplicity) were analyzed using a nonparametric rank sum test. To apply the test, a single functional response curve was fitted to the pooled samples, and regression residuals were computed, keeping track of which residuals were from the third instars and which were from the adult female or male stages. The residuals from each stage were tested using the Kruskal-Wallis test (Holander and Wolfe 1973, Gibbons 1976, Houck and Strauss 1985). The Kruskal-Wallis test was also used to determine differences in prey consumption among third instars, adult females, and adult males for a given prey density. When there was a significant difference among the treatments, the Mann-Whitney test was used for pairwise comparisons with the Bonferroni correction ($P = 0.05/3 = 0.0167$) (Siegel and Castellan

Table 1. Estimates of the linear coefficient, $P_1 \pm$ SE, and the probability (P) that $P_1 \neq 0$ in the reduced logistic model of equation 1 used to determine the type of functional response exhibited by _C. septempunctata_ and _H. axyridis_ when preying on soybean aphid, _A. glycines_, at $26 \pm 1°C$ in a 24-h prey exposure period

Predator	Stage	$P_1 \pm$ SE	P ($P_1 \neq 0$)
C. septempunctata	Third instars	-0.0430 ± 0.0099	0.0001
	Females	-0.0228 ± 0.0100	0.0262
	Males	-0.0371 ± 0.0107	0.0010
H. axyridis	Third instars	-0.0351 ± 0.0071	<0.0001
	Females	-0.0338 ± 0.0082	0.0001
	Males	-0.0411 ± 0.0078	<0.0001

Estimates were obtained by rewriting the reduced logistic model to a quadratic, followed by quadratic curve estimation regression.

1988, SPSS 2006). All analyses were performed using SPSS software (SPSS 2006).

Results

Functional Response. The cubic equation for third instars, adult females, and adult males of _C. septempunctata_ and _H. axyridis_ yielded nonsignificant cubic parameters; therefore, these terms were eliminated and the remaining parameters were retested. The linear coefficient, P_1, in the reduced logistic model was significantly negative for third instars, adult females, and adult males for both _C. septempunctata_ and _H. axyridis_ (Table 1), indicating that all stages tested of both species exhibited a type II response to soybean aphids.

The parameter estimates of the instantaneous searching rate (a) and the handling time per prey item (T_h) for both the Holling's disc equation and the random predator equation for _C. septempunctata_ and _H. axyridis_ are presented in Table 2. Data for all three stages of both lady beetles fit the Holling's disc model well, but not the random predator model for which the asymptotic 95% CIs of T_h estimates included zero.

The Holling's disc equation with corresponding a and T_h for _C. septempunctata_ (Table 2) predicts theoretical maximum predation rates of 204, 277, and 166 adult aphids per day for third instars, female adults, and male adults, respectively.

The functional response curve for adult males of _C. septempunctata_ was significantly different from those of third instars (Mann-Whitney test, $Z = -5.882$, $P < 0.001$) and adult females ($Z = -6.687$, $P < 0.001$). However, there was no significant difference between the curves of third instars and adult females ($Z = -0.995$, $P = 0.32$; Fig. 1).

The Holling's disc equation predicts that, at an aphid density of 250 aphids per arena, the maximum number of prey consumed by third instars, adult females, and adult males would be 119, 135, and 89, respectively, for _C. septempunctata_ and 134, 106, and 61, respectively, for _H. axyridis._

Third instars of _C. septempunctata_ consumed significantly more aphids than did male adults at all prey densities, except at 120 aphids per plant (Table 3). Females consumed significantly more prey than did males at all prey densities except at 30 and 90 aphids/

Table 2. Estimates of the instantaneous searching rate (*a*) and handling time (*T_h*) of *C. septempunctata* and *H. axyridis* when preying on soybean aphid, *A. glycines*, at 26 ± 1°C in a 24-h prey exposure period with asymptotic 95% confidence intervals using the Holling's disc and random predator models

Predator	Stage	Equation	R^2	a	95% CI of a	T_h	95% CI of T_h
C. septempunctata	Third instars	Holling's disc	0.7192	1.1578	0.8440–1.4715	0.0049	0.0031–0.0067
		Random predator	0.6456	0.5574	0.1731–0.9418	−0.0096	−0.0239–0.0047
	Females	Holling's disc	0.8210	1.0536	0.8337–1.2735	0.0036	0.0021–0.0051
		Random predator	0.7692	0.8210	0.4005–1.2415	−0.0043	−0.0118–0.0032
	Males	Holling's disc	0.5884	0.7722	0.5009–1.0436	0.0060	0.0025–0.0094
		Random predator	0.6365	0.2420	0.0578–0.4261	−0.0248	−0.0551–0.0055
H. axyridis	Third instars	Holling's disc	0.8343	1.2079	0.9702–1.4457	0.0041	0.0028–0.0053
		Random predator	0.7334	1.0185	0.4861–1.5509	−0.0023	−0.0086–0.0041
	Females	Holling's disc	0.7671	1.3231	1.0132–1.6330	0.0064	0.0050–0.0078
		Random predator	0.5257	0.7810	0.3383–1.2238	−0.0023	−0.1027–0.0056
	Males	Holling's disc	0.5767	1.4460	0.9744–1.9176	0.0136	0.0114–0.0157
		Random predator	−0.1699	0.3135	0.0392–0.5879	0.0111	−0.0371–0.0149

plant. There were no significant differences in prey consumed between third instars and females at any prey density.

The functional response curves of larvae, adult females, and adult males of *H. axyridis* were significantly different from each other (Mann-Whitney test: Z = −4.393, *P* < 0.001 between larvae and adult females; Z = −7.988, *P* < 0.001 between larvae and adult males; Z = −5.811, *P* < 0.001 between adult females and males; Fig. 1).

The Holling's disc equation with corresponding *a* and *T_h* for *H. axyridis* (Table 2) predicts theoretical maximum predation rates of 244, 156, and 73 adult aphids per day for third instars, adult females, and adult males, respectively.

Third instars of *H. axyridis* consumed significantly more aphids than did adult males at all prey densities (Table 3). Females consumed significantly more prey than did males at all prey densities except at 30 aphids/plant. There were no significant differences in prey consumed between third instars and females at all prey densities, except at 150 aphids/plant.

When functional response curves of *C. septempunctata* and *H. axyridis* were compared between the same stage or same sex, they were significantly different for larvae (Mann-Whitney test: Z = −2.715, *P* = 0.007) and adult females (Z = −2.473, *P* = 0.013). There was no significant difference between the shapes of the functional response curves of adult males of each species (Z = −1.793, *P* = 0.073).

Predation of *C. septempunctata* and *H. axyridis* on Soybean Plants at V3 Stage. Whereas third instars and adult females consumed significantly more prey than did adult males for both *C. septempunctata* and *H. axyridis* (Fig. 2), there were no significant differences in number of prey consumed by third instars and adult females. Comparisons of predation between the same stages of *C. septempunctata* and *H. axyridis* showed that there were no significant differences between species for a given stage: larvae (Mann-Whitney test: Z = −0.958, *P* = 0.338), adult females (Z = −0.303, *P* = 0.762), and adult males (Z = −0.454, *P* = 0.650).
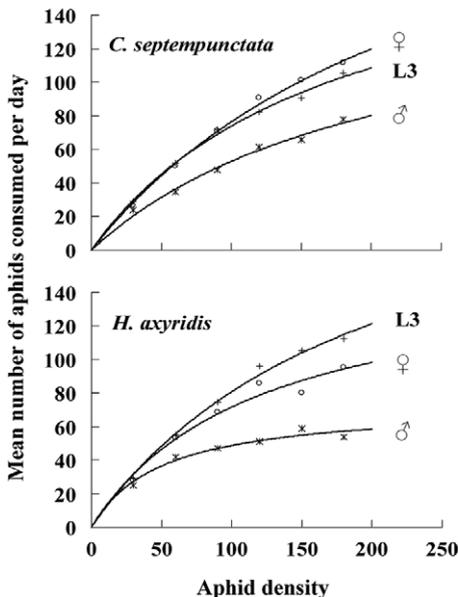

Fig. 1. Functional responses of third instars (L3), adult females, and adult males of *C. septempunctata* and *H. axyridis* to adult *A. glycines* in a 24-h prey exposure period at 26 ± 1°C.

Table 3. Mean ± SE numbers of adult soybean aphid, *A. glycines*, consumed by *C. septempunctata* and *H. axyridis* third instars, adult females, and adult males at different prey densities on excised soybean plants at the V1 stage at 26 ± 1°C in a 24-h prey exposure period

Predator[a]	Prey density	Mean ± SE numbers of aphids consumed		
		Third instars	Females	Males
C. septempunctata	30	28.7 ± 0.3a	26.63 ± 1.2ab	23.8 ± 1.9b
	60	51.6 ± 2.0a	50.13 ± 2.2a	34.6 ± 3.2b
	90	71.9 ± 4.0a	71.23 ± 2.4ab	47.6 ± 6.8b
	120	82.3 ± 7.2ab	90.80 ± 4.2a	61.6 ± 4.9b
	150	90.8 ± 7.9a	101.0 ± 7.1a	65.8 ± 6.5b
	180	105.4 ± 6.4a	115.0 ± 6.6a	77.8 ± 9.7b
H. axyridis	30	28.9 ± 0.2a	27.9 ± 0.5ab	25.0 ± 1.1b
	60	55.3 ± 0.8a	53.1 ± 1.3a	41.8 ± 3.1b
	90	74.7 ± 1.7a	68.5 ± 3.1a	47.2 ± 2.8b
	120	95.8 ± 3.5a	85.9 ± 4.8a	51.2 ± 2.5b
	150	105.4 ± 6.8a	80.2 ± 5.0b	58.8 ± 3.7c
	180	112.4 ± 6.8a	95.2 ± 5.0a	53.7 ± 3.5b

[a] For a specific predator, means within the same prey density followed by the same letter are not significantly different (Kruskal-Wallis test followed by Mann-Whitney test with Bonferroni correction, *P* > 0.05/3 = 0.0167).
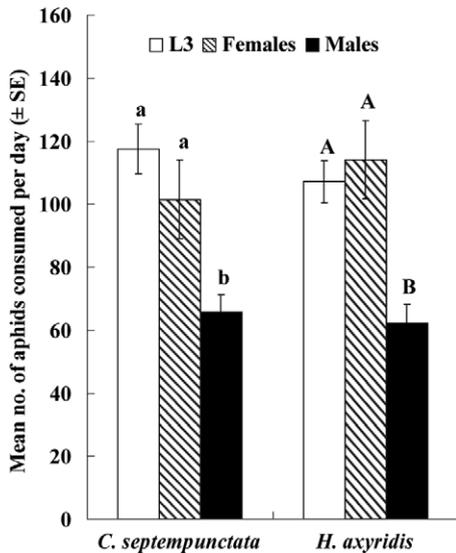
Fig. 2. Number of *A. glycines* consumed by third instars (L3), adult females, and adult males of *C. septempunctata* and *H. axyridis* on V3 stage soybean plants in a 24-h prey exposure period at 26 ± 1°C with an initial aphid density of 250 aphids per plant. For each lady beetle species, bars with the same letter were not significantly different among life stages (Kruskal-Wallis test followed by Mann-Whitney test with Bonferroni correction, $P > 0.05/3 = 0.0167$). No differences between species were significant for any life stage ($P > 0.05$).

Discussion

All stages of *C. septempunctata* and *H. axyridis* examined against soybean aphid showed a type II functional response to soybean aphid prey. Type II functional response curves have been reported in previous studies of *C. septempunctata* and *H. axyridis* predation on aphids (Sinha et al. 1982; Carter et al. 1984; Hu 1992; Xue et al. 1996; Skirvin et al. 1997; Wang et al. 1999; Ma et al. 2000; Liu et al. 2002; Xia et al. 2003; Zhang et al. 2004, 2007; Ge et al. 2006; Zhang and Liu 2006). Type II functional response indicates that the number of prey consumed increases with increasing prey density, but the rate of consumption decreases with increasing prey density.

Predictions of prey consumption using Holling's disc model at a density of 250 aphids per arena were very similar to those observed experimentally on V3 soybean plants (Fig. 2). However, the arena and plant surface area in that experiment were considerably greater than that of the functional response arena from which the predicted values were derived, indicating that both *C. septempunctata* and *H. axyridis* are efficient at searching for, and consuming, soybean aphids.

Third instars and female adults of both coccinellids were more voracious than adult males, likely because of higher nutritional requirements for development of the larval stage and for reproduction by female adults (Omkar and Srivastava 2003). *C. septempunctata* and *H. axyridis* exhibited similar voracity and response to soybean aphid density, which may in part be related to their similar body sizes.

The random predator equation has been considered more appropriate than Holling's disc equation in studies where consumed prey are not replaced and trial duration is relatively long and leads to a significant reduction in prey density over time (Houck and Strauss 1985). However, our data fit Holling's disc equation well, but not the random predator equation. Similar results have been found in other studies. The instantaneous searching rate (*a*) of first instars of *H. axyridis* attacking the cotton aphid was 0.0037 ± 0.00617 (Lee and Kang 2004), indicating the data did not fit the random predator model. Zamani et al. (2006) reported that the type II functional responses of two aphid parasitoids, *Aphidius colemani* and *A. matricariae,* to the cotton aphid were best described using Holling's disc equation rather than the random predator equation. Fan and Petitt (1994, 1997) found that the Holling's disc equation has been used most commonly to describe the type II functional response, although it has been criticized by Royama (1971) and Rogers (1972). Rogers (1972) acknowledged that both equations can be used to describe the same results but that the resultant estimates of instantaneous searching rate and handling time will be different because of different assumptions made in each. The random predator equation assumes a random search pattern, whereas the disc equation assumes a systematic search pattern with no area searched more than once. Consequently, the instantaneous searching rate (*a*) calculated from the random predator equation is greater than that calculated from the disc equation. Our results and the results above indicate that searching behavior of *C. septempunctata* and *H. axyridis* is not random, but systematic, probably because of the use of semiochemical cues (Magro et al. 2007).

The predation capacity of a specific coccinellid varies with the prey species. We predicted theoretical maximum values of predation of 204 and 277 adult soybean aphids per third instar and female adult per day, respectively. Xia et al. (2003) reported that *C. septempunctata* had a handling rate of 120 adult cotton aphids per third instar per day and 206 per adult female per day at similar temperatures to our study.

When evaluating the potential for a particular predator as a biological control agent, it is critical to assess its predation capacity (Lucas et al. 1997). Quantitative models of interactions between predator and prey can be used to predict prey–predator dynamics (Hassell 1978). *H. axyridis* and *C. septempunctata* are known predators of soybean aphid throughout its North American range (Rutledge et al. 2004, Costamagna and Landis 2007); assuming no great genetic differences among populations that impact predation capacity, our results have the potential to help quantify impact of these predators on soybean aphid populations outside our study area. These predators have high predation capacity and great potential to suppress soybean populations, which suggests that the development of dynamic action thresholds that incorporate natural enemy numbers is warranted. Dynamic action thresholds could be developed based on functional response curves and predation capacities of key

predators in conjunction with projections of aphid population growth under given environmental conditions. However, field studies will be needed to validate the dynamic action threshold, because laboratory studies may not accurately reflect field predation rates. Giving consideration to field observations of both aphid and lady beetle populations before making an insecticide application has the potential to reduce insecticide use against the soybean aphid, as well as to help preserve natural enemy populations.

Acknowledgments

References Cited

Baute, T. 2007. Soybean aphid. Ontario Ministry of Agriculture and Rural Affairs Factsheet, Agdex# 622/141. (htpp://www.omafra.gov.on.ca/english/crops/facts/04-059.htm).

Carter, M. C., D. Sutherland, and A.F.G. Dixon. 1984. Plant structure and the searching efficiency of coccinellid larvae. Oecologia (Berl.) 63: 394–397.

Chang, Y. D., J. Y. Lee, and Y. N. Youn. 1994. Primary parasitoids and hyperparasitoids of the soybean aphid, *Aphis glycines* (Homoptera: Aphididae). Korean J. Appl. Entomol. 33: 51–55.

Chen, C., Z. Tang, and X. Li. 2005. Studies on predation of *Coccinella septempunctata* to *Aphis citricola.* Entomol. J. East China 14: 162–164.

Costamagna, A. C., and D. A. Landis. 2006. Predators exert top-down control of soybean aphid across a gradient of agricultural management systems. Ecol. Appl. 16: 1619–1628.

Costamagna, A. C., and D. A. Landis. 2007. Quantifying predation on soybean aphid through direct field observations. Biol. Control 42: 16–24.

Costamagna, A. C., D. A. Landis, and C. D. Difonzo. 2007. Suppression of soybean aphid by generalist predators results in a trophic cascade in soybeans. Ecol. Appl. 17: 441–451.

Fan, Y., and F. L. Petitt. 1994. Parameter estimation of functional response. Environ. Entomol. 23: 785–794.

Fan, Y., and F. L. Petitt. 1997. Functional response, variance, and regression analysis: a reply to Williams and Juliano. Environ. Entomol. 26: 1–3.

Fox, T. B., D. A. Landis, F. F. Cardoso, and C. D. Difonzo. 2004. Predators suppress *Aphis glycines* Matsumura population growth in soybean. Environ. Entomol. 33: 608–618.

Fox, T. B., D. A. Landis, C. D. Difonzo, and F. F. Cardoso. 2005. Impact of predation on establishment of the soybean aphid, *Aphis glycines* in soybean, *Glycine max.* BioControl 50: 545–563.

Ge, Y., L. Wan, and S. Zhao. 2006. Predation of *Harmonia axyridis* Pallas on *Rhopalosiphum nymphaeae* Linne (Homoptera:Aphididae). Acta Agri.Univ. Jiangxiensis (Nat. Sci. Ed.) 28: 208–212.

Gibbons, J. D. 1976. Nonparametric methods for quantitative analysis. Holt, Rinehart and Winston, New York.

Hao, D. Q., and D. D. Hao. 2005. Study on the functional response of *Coccinella septempunctata* L. to *Myzus persicae.* J. Agric. Sci. 26: 18–20.

Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton, NJ.

Heimpel, G. E., D. W. Ragsdale, R. Venette, Z. Wu, K. R. Hopper, R. J. O'Neil, and C. E. Rutledge. 2004. Prospects for importation biological control of the soybean aphid: anticipating potential costs and benefits. Ann. Entomol. Soc. Am. 97: 249–258.

Holander, M., and D. A. Wolfe. 1973. Nonparametric statistical methods. Wiley, New York.

Holling, C. S. 1959a. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Can. Entomol. 91: 293–320.

Holling, C. S. 1959b. Some characteristics of simple types of predation and parasitism. Can. Entomol. 91: 385–398.

Hou, M. L., and F. H. Wan. 2004. Predation of *Myzus persicae* by adults of *Coccinella septempunctata.* Entomol. Know. 41: 347–350.

Houck, M. A., and R. E. Strauss. 1985. The comparative study of functional responses: experimental design and statistical interpretation. Can. Entomol. 117: 617–629.

Hu, G. 1992. Functional responses of larvae of three ladybirds, *Adonia variegata, Coccinella septempunctata* and *C. transversogutata* to the aphid *Schizaphis graminum* (Homop: Aphididae). Nat. Enemies Insects 14: 180–185.

Juliano, S. A. 2001. Nonlinear curve-fitting: predation and functional response curves, pp. 178–196. *In* S. M. Scheiner and J. Gurevitch (eds.), Design and analysis of ecological experiments, 2nd ed. Oxford University Press, New York.

Kumar, A., N. Kumar, A. Siddiqui, and A. Tripathi. 1999. Prey-predator relationship between *Lipaphis erysimi* Kalt. (Hom., Aphididae) and *Coccinella septempunctata* L. (Col., Coccinellidae). II. Effect of host plants on the functional response of the predator. J. Appl. Entomol. 123: 591–596.

Lee, J.-H., and T.-J. Kang. 2004. Functional response of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) to *Aphis gossypii* Glover (Homoptera: Aphididae) in the laboratory. Biol. Control 31: 306–310.

Liu, J., X. Wu, Q. Sha, Z. Tan, and J. Deng. 2002. Functional responses and density interference effect in *Harmonis axyridis* Pallas, a predator to *Myzus nicotianae* (Blackman). J. Southwest Univ. (Nat. Sci. Ed) 24: 433–435.

Liu, J., K. Wu, K. Zhao, and K. R. Hopper. 2004. Population dynamics of *Aphis glycines* (Homoptera: Aphididae) and its natural enemies in soybean in northern China. Ann. Entomol. Soc. Am. 97: 235–239.

Livdahl, T. P., and A. E. Stiven. 1983. Statistical difficulties in the analysis of predator functional response data. Can. Entomol. 115: 1365–1370.

Lou, H. H. 1987. Functional response of *Harmonia axyridis* to the density of *Rhopalosiphum prunifoliae.* Nat. Enemies Insects 9: 84–87.

Lucas, E., D. Coderre, and C. Vincent. 1997. Voracity and feeding preferences of two aphidophagous coccinellids on *Aphis citricola* and *Tetranychus urticae.* Entomol. Exp. Appl. 85: 151–159.

Ma, F., F. Lu, C. Wei, Y. Zou, X. Cheng, and H. Wu. 2000. Predatism of *Harmonia axyridis* adults on different ranges of starvation to *Myzus persicae.* J. Anhui Agric. Univ. 27: 348–351.

Magro, A., J. N. Téné, N. Bastin, A.F.G. Dixon, and J. L. Hemptinne. 2007. Assessment of patch quality by ladybirds: relative response to conspecific and heterospecific larval tracks a consequence of habitat similarity? Chemoecology 17: 37–45.

Miao, J., K. Wu, K. R. Hopper, and G. Li. 2007. Population dynamics of *Aphis glycines* (Homoptera: Aphididae) and impact of natural enemies in northern China. Environ. Entomol. 36: 840–848.

[NCSRP] North Central Soybean Research Program, Plant Health Initiative. 2006. Soybean aphid management. (http://www.planthealth.inf/aphids_mgmnt.htm).

Omkar, and S. Srivastava. 2003. Functional response of the seven-spotted lady beetle, *Coccinella septempunctata* Linnaeus on the mustard aphid, *Lipaphis erysimi* (Kaltenbach). Insect Sci. Appl. 23: 149–152.

Quimio, G. M., and J. Calilung. 1993. Survey of flying viruliferous aphid species and population build-up of *Aphis glycines* Matsumura in soybean fields. Philippine Entomol. 9: 52–100.

Ragsdale, D. W., B. P. McCornack, R. C. Venette, B. D. Potter, I. V. MacRae, E. W. Hodgson, M. E. O'Neal, K. D. Johnson, R. J. O'Neil, C. D. DiFonzo, T. E. Hunt, P. A. Glogoza, and E. M. Cullen. 2007. Economic threshold for soybean aphid (Hemiptera: Aphididae). J. Econ. Entomol. 100: 1258–1267.

Rogers, D. 1972. Random search and insect population models. J. Anim. Ecol. 41: 369–383.

Royama, T. 1971. A comparative study of models for predation and parasitism. Res. Popul. Ecol. Suppl. 1: 1–91.

Rutledge, C. E. 2004. First record of the soybean aphid, *Aphis glycines* (Hemiptera: Sternorrhyncha: Aphididae) in Connecticut and Massachusetts. Great Lakes Entomol. 37: 198–201.

Rutledge, C. E., and R. J. O'Neil. 2005. *Orius insidiosus* (Say) as a predator of the soybean aphid, *Aphis glycines* Matsumura. Biol. Control 33: 56–64.

Rutledge, C. E., R. J. O'Neil, T. B. Fox, and D. A. Landis. 2004. Soybean aphid predators and their use in integrated pest management. Ann. Entomol. Soc. Am. 97: 240–248.

Siegel, S., and J. C. Castellan. 1988. Nonparametric statistics for behavioral sciences. McGraw-Hall, New York.

Sinha, T. B., R. K. Pandey, R. Singh, C.P.M. Tripathi, and A. Kumar. 1982. The functional response of *Coccinella septempunctata* Linn, a coccinellid predator of mustard aphid, *Lipaphis erysimi* Kalt. Entomon 7: 7–10.

Skirvin, D. J., J. N. Perry, and R. Harrington. 1997. A model describing the population dynamics of *Sitobion avenae* and *Coccinella septempunctata.* Ecol. Model. 96: 29–39.

Solomon, M. E. 1949. The natural control of animal populations. J. Anim. Ecol. 18: 1–35.

SPSS. 2006. SPSS for Windows, version 15.0. SPSS, Chicago, IL.

Tully, T., P. Cassey, and R. Ferriere. 2005. Functional response: rigorous estimation and sensitivity to genetic variation in prey. Oikos 111: 479–487.

van den Berg, D.A.H., A. Muhammad, R. Rusli, A. Widayanto, H. B. Wirasto, and I. Yully. 1997. Evaluating the role of predation in population fluctuations of the soybean aphid *Aphis glycines* in farmers' fields in Indonesia. J. Appl. Ecol. 34: 971–984.

Venette, R. C., and D. W. Ragsdale. 2004. Assessing the invasion by soybean aphid (Homoptera: Aphididae): where will it end? Ann. Entomol. Soc. Am. 97: 219–226.

Wang, J., Y. Wang, and S. Sun. 1999. Functional responses of ladybirds (*Coccinella septempunctata* L.) to the aphids: *Aphis robiniae* Macchiati and *A. citricola* van der Goot. J. Beijing Agric. Coll. 14: 19–23.

Watson, D. M., T. Y. Du, M. Li, J. J. Xiong, D. G. Liu, M. D. Huang, D. J. Rae, and G.A.C. Beattie. 2000. Functional responses of, and mutual interference in *Aleurodothrips fasciapennis* (Franklin) (Thysanoptera: Phlaeothripidae) and implications for its use as a biocontrol agent. Gen. Appl. Entomol. 29: 31–37.

Wu, Z., D. W. Ragsdale, G. E. Heimpel, D. Schenk-Hamlin, and W. Zhan. 2004. The soybean aphid in China: a historical review. Ann. Entomol. Soc. Am. 97: 209–218.

Xia, J. Y., R. Rabbinge, and W. Van Der Werf. 2003. Multistage functional responses in a ladybeetle-aphid system: scaling up from the laboratory to the field. Environ. Entomol. 32: 151–162.

Xue, M., Z. Li, Q. Li, and A. Liu. 1996. Study on predatory function of *Coccinella septempunctata* to the cruciferous vegetable aphids (*Lipaphis enysimi* and *Myzus persicae*). J. Shandong Agri. Univ. (Nat. Sci.) 27: 171–175.

Zamani, A., A. Talebi, Y. Fathipour, and V. Baniameri. 2006. Temperature-dependent functional response of two aphid parasitoids, *Aphidius colemani* and *Aphidius matricariae* (Hymenoptera: Aphidiidae), on the cotton aphid. J. Pest Sci. 79: 183–188.

Zhang, A., J. Fen, Y. Yu, S. Zhang, and Z. Li. 2004. The functional response of *Coccinella septempunctata* and *Chrysopa septempunctata* to *Hyalopterus amygdali.* Entomol. J. East China 13: 69–71.

Zhang, R., F. Yang, and J. Ma. 2007. Studies on predation of *Coccinella septempunctata* on *Therioaphis trifolii.* Plant Protect. 33: 42–45.

Zhang, Y., and S. Liu. 2006. Predation of *Harmonia axyridis* (Pallas) on aphid species, *Chaitophorus populeti* (Panzer), *Rhopalosiphum padi* (Linnaeus) and *Lipaphis erysimi* (Kalteback). Chinese Agric. Sci. Bull. 22: 323–326.