Effect of temperature on the functional response of *Adalia bipunctata* to *Myzus persicae*

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Abstract The effect of temperature on the functional response of female adults of the two-spot ladybird, *Adalia bipunctata* L. (Coleoptera: Coccinellidae) was examined in petri dish arenas containing sweet pepper leaves infested with different densities of the green peach aphid, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae). The predator showed a type II functional response at three tested temperatures ranging from 19°C to 27°C. The theoretical maximum number of prey captured by the predator increased with temperature. Based on the random predator equation, the estimated attack rates ranged from 0.13 h^{-1} at 19°C to 0.35 h^{-1} at 27°C on a leaf area of 20–25 cm^2. There was no significant difference between the attack rates of the predator at 23°C and 27°C. Handling time significantly decreased as temperature increased from 19°C (0.39 h) to 27°C (0.24 h). This study shows that *A. bipunctata* displays high predation rates on *M. persicae* for a wide range of temperatures, indicating its potential for augmentative releases against this aphid pest. The limitations of the predictions generated by functional response experiments are discussed.

Introduction

A quantitative and qualitative understanding of the interaction among different species is crucial for the management of agricultural pests. Each species in an agricultural ecosystem is part of an often complex community, where it has to interact with many other species. These interactions may be competitive, predatory, parasitic or mutualistic (Begon et al. 1996; Bellows and Hassell 1999). One of the most important interactions with implications for biological control is the predator–prey relationship. How predators respond to changes in prey availability (i.e., functional response) is an issue of particular interest (Jeschke et al. 2002) and can determine whether a predator is able to regulate the density of its prey (Murdoch and Oaten 1975). The functional response has traditionally been defined as the number of prey attacked by an individual natural enemy in relation to host density over a given time interval (Solomon 1949). The response is characterized by an increase in

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the number of prey (or hosts) attacked over the lower range of prey densities, and an upper limit to the number of prey attacked at higher prey densities due to satiation in the case of predators (Mills 1982; Jeschke et al. 2002) and egg limitation or handling time constraints in the case of parasitoids (Getz and Mills 1996; Mills and Lacan 2004). Basically, functional responses have been delimited to three different types (Holling 1959). A type I response is characterized by a linear increase, a type II response by a monotonic decelerating increase, and a type III response by a sigmoidal increase in host numbers attacked. The type II functional response is the most frequently reported type in insects (Hassell et al. 1976; Begon et al. 1996), including coccinellids (Hodek and Honek 1996; Dixon 2000). However, predators may show different types of functional response curves as a function of host plant (Messina and Hanks 1998; De Clercq et al. 2000) or prey type (Sarmento et al. 2007). *Harmonia axyridis* (Pallas) has been reported to exhibit type I (Lou 1987), type II (He et al. 1994), and type III (Hu et al. 1989) functional responses on different aphid species. Interestingly, third instars and adults of *H. axyridis* exhibited different types of responses (type II and I, respectively) on the eggs of the monarch butterfly, *Danaus plexippus* (L.) (Koch et al. 2003).

In order to model predation by a long-lived, polyphagous predator, it is essential to know how the key parameters of the functional response (i.e., the attack coefficient, a, and handling time, T_h) scale with temperature (Thompson 1978). However, there are few data showing the influence of temperature on type and magnitude of the functional response of coccinellid predators. Overall, the predation rate of larval and adult stages of coccinellids has been reported to increase with temperature within a range of ca. 10–30°C (Mack and Smilowitz 1982a, b; Giroux et al. 1995; Xia et al. 2003; Gotoh et al. 2004).

The two-spotted ladybird beetle, *Adalia bipunctata* (L.), is a common natural enemy of aphids in Europe and Central Asia (Mills 1979; Majerus 1994) and has been considered a potential biological control agent in different agro-ecosystems (Majerus 1994; Hodek and Honek 1996; Dixon 2000; Omkar and Pervez 2005). Although some studies have investigated the functional response of *A. bipunctata* (Mills 1979, 1982; Hemptinne et al. 1996), none of them have addressed the effect of temperature on the functional

response of the predator. Mills (1979, 1982) found that prey consumption by female adults of *A. bipunctata* increased curvilinearly suggesting a type II functional response. On the contrary, the males of this species were not found to show a functional response (Hemptinne et al. 1996).

The objective of the current study is to investigate the effects of temperature on the functional response of *A. bipunctata* to different densities of the green peach aphid, *Myzus persicae* (Sulzer). Improving our understanding of the predator–prey interactions between *A. bipunctata* and *M. persicae* may be helpful to optimize biological control of this economically important aphid pest.

Materials and methods

Insects

Adults of *A. bipunctata* were taken from a colony at the Laboratory of Agrozoology, Ghent University, which was started with larvae purchased from Biobest NV (Westerlo, Belgium). At the commercial facility, the ladybird had been fed with live pea aphids, *Acyrthosiphon pisum* (Harris). Upon introduction at the Laboratory of Agrozoology, the predator was reared for one generation on an ad libitum supply of different nymphal stages of the green peach aphid, *M. persicae*, at each of the examined temperatures before starting the functional response study. The aphids were reared on sweet pepper plants (*Capsicum annuum* L., cv. California Wonder) in a culture room at 25 ± 2°C, 50 ± 10% RH, and a photoperiod of 16:8 (L:D) h.

Functional response experiment

The experiment was performed at three constant temperatures (19, 23 and 27 ± 1°C), a relative humidity of 65 ± 5% and a photoperiod of 16:8 (L:D) h. The selected temperatures should reflect thermal conditions frequently experienced by the predator in different protected and field crops in temperate areas. The female *A. bipunctata* used in the experiment had body weights ranging from 12.1 to 13.4 mg. At each of the tested temperatures, females were used that had initiated oviposition (i.e., 8–

10 days old). To standardize the response, predators were starved for 24 h in boxes containing only a source of moisture before release into the test arena. The experimental arena consisted of a plastic Petri dish (14 cm in diameter) lined with paper towel. Each dish contained a sweet pepper leaf with its petioles inserted into an Eppendorf tube (2 ml) filled with water. The average leaf area (both sides) was estimated to be approximately 20–25 cm^2 ($n = 5$ leaves). Third and fourth instars of *M. persicae* were used as prey in the experiment. Aphids were gently transferred by a fine camel hair brush from plants of the stock culture to the leaves in the test arenas. Prey densities used were: 5, 10, 15, 20, 30, 60, 80, 100 and 130 aphids per leaf. The aphids were allowed to settle and a female adult predator was introduced in each Petri dish. At each prey density, there were ten replicates for predator treatments and five controls (i.e., arenas without a predator). The total number of prey killed during a 24-h period was recorded. Killed prey were not replaced during the experiment (prey depletion method). Predation mortality was corrected for control mortality using the formula given by Xia et al. (2003):

$$N_e = N_0 \frac{N_d - N_c}{N_0 - N_c}, \qquad (1)$$

where N_e represents the number of prey killed, N_0 represents the initial number of prey, N_d represents the number of prey eaten and dead in the treatment, and N_c represents the number of prey dead in the control.

Data analysis

Data were analysed using SPSS (SPSS Inc. 2006) for analysis of variance (ANOVA) and SAS (SAS Institute 1999) for analysis of functional response. Data were submitted to a two-way ANOVA for the significance of the main effects of prey density and temperature on predation and their interaction.

Analysis of the functional response consists of two distinctive steps (De Clercq et al. 2000; Juliano 2001): determination of the type of functional response and estimation of the parameters of the functional response curve. The shape of the functional response is determined by a logistic regression of the proportion of prey eaten as a function of initial density. This is done by fitting a polynomial function:

$$\frac{N_e}{N_0} = \frac{\exp(P_0 + P_1 N_0 + P_2 N_0{}^2 + P_3 N_0{}^3)}{1 + \exp(P_0 + P_1 N_0 + P_2 N_0{}^2 + P_3 N_0{}^3)}, \qquad (2)$$

where N_e is the number of prey eaten, N_0 is the initial number of prey, and P_0, P_1, P_2, and P_3 are the parameters to be estimated. To estimate these parameters, the CATMOD procedure was used (Juliano 2001). The data sets were individually fitted to the model (2), for determining the type of functional response (type II or III). The sign of P_1 and P_2 can be used to distinguish the shape of the curves. A positive linear parameter (P_1) and a negative quadratic parameter (P_2) indicate that the functional response is type III, whereas if both parameters are negative, the functional response is type II (Juliano 2001). In the second step, a nonlinear least square regression (NLIN) procedure was used to estimate the parameters of the random predator equation (T_h and a for type II and b, c, and d for type III) (Rogers 1972; Juliano 2001). These equations are described by:

$$N_e = N_0\{1 - \exp[a(T_h N_e - T)]\} \quad \text{(type II, prey depletion)}, \qquad (3)$$

$$N_e = N_0\{1 - \exp[(d + bN_0)(T_h N_e - T)/(1 + cN_0)]\} \quad \text{(type III, prey depletion)}, \qquad (4)$$

where N_e is the number of prey eaten, N_0 the initial number of prey, a the attack constant, T the total time available (24 h) and T_h the handling time per prey, and b, c, and d are constants. Lower densities where prey were completely depleted by the end of the experiment were omitted from the analysis to avoid biased estimates (as discussed below). Separation of statistically different parameter estimates was done using asymptotic 95% confidence intervals (CI) (Juliano 2001).

Results

The proportion of prey consumed by the predator declined with increasing prey density, justifying the decision to use non-linear curve fitting (Table 1). The negative linear coefficient ($P_1 < 0$) suggests that there was a type II functional response at 19°C. Because estimates of the linear coefficient in the original cubic model were not significantly

Table 1 Results of logistic regression analysis of the proportion of *M. persicae* nymphs (3rd and 4th instars) eaten by adult females of *A. bipunctata* on initial prey density at different temperatures

Temperature (°C)	Coefficient	Estimate	SE	χ^2	P-value
19	Constant (P_0)	6.7094	0.8607	60.7704	<0.0001
	Linear (P_1)	−0.1911	0.0336	32.3628	<0.0001
	Quadratic (P_2)	0.0019	0.0004	20.1901	<0.0001
	Cubic (P_3)	−6.21E-6	1.591E-6	15.2199	<0.0001
23	Constant (P_0)	−3.7786	4.0637	0.8646	0.3524
	Linear (P_1)	0.2378	0.1375	2.9906	0.0837
	Quadratic (P_2)	−0.0032	0.0015	4.6605	0.0309
	Cubic (P_3)	0.12E-4	5.188E-6	5.6793	0.0172
27	Constant (P_0)	2.1165	6.3683	0.1105	0.7396
	Linear (P_1)	0.0910	0.2120	0.1844	0.6676
	Quadratic (P_2)	−0.0016	0.0023	0.5232	0.4695
	Cubic (P_3)	6.568E-6	7.798E-6	0.7096	0.3996

different from 0 ($P > 0.05$) in the case of 23°C and 27°C, the model was reduced by subsequently omitting the cubic term until all remaining coefficients were significant (Juliano 2001; Mahdian et al. 2006). The negative sign of the estimates of the linear coefficient (P_1) in the reduced models for 23°C (quadratic model: $P_1 = -0.0884$, $P < 0.0001$) and 27°C (quadratic model: $P_1 = -0.0869$, $P < 0.0001$) indicated a type II functional response. Significant quadratic terms ($P2$) were derived for *A. bipunctata* at temperatures ranging from 19°C to 23°C, indicating that asymptotically declining proportions of prey were killed by the predator at these temperatures.

All data were fitted to the random predator equation. The coefficients of determination (R^2) indicated greater variation in predation rates at 23°C than at 19°C and 27°C (Table 2). The number of *M. persicae* nymphs killed by *A. bipunctata* females increased at a decreasing rate until reaching an upper plateau, as the number of *M. persicae* offered increased (Fig. 1). The theoretical maximum number of prey captured by the predator increased with temperature. A two-way ANOVA with prey density and temperature as factors revealed a significant difference in predation at the different prey densities ($F_{8,243} = 878.90$, $P < 0.001$) and across temperatures ($F_{2,243} = 185.54$, $P < 0.001$). The interaction between the two factors was also significant ($F_{16,243} = 30.54$, $P < 0.001$).

The relationship between temperature, handling times and attack rates, calculated from the response curves, is shown in Table 2. Handling time significantly decreased ($F_{2,29} = 344.083$, $P < 0.001$) as temperature increased from 19°C (0.39 h) to 27°C (0.24 h). Likewise, there was a significant effect of temperature on attack rate ($F_{2,29} = 26.414$, $P < 0.001$). Attack rate on a 20–25 cm² leaf area at 23°C (0.31 h^{-1}) was higher than that at 19°C (0.13 h^{-1}), but similar to that at 27°C (0.35 h^{-1}). The estimated maximum numbers of 3rd–4th instars of *M. persicae* that can be killed by a single *A. bipunctata* female (T/T_h) were 2.56, 2.78 and 4.17 per hour, at 19, 23 and 27°C, respectively.

Table 2 Parameters estimated by the random predator equation and corresponding asymptotic 95% confidence intervals (CI) indicating functional response of adult females of *A. bipunctata* to densities of *M. persicae* 3rd–4th instars at different temperatures

Temperature (°C)	Type	R^2	a (h^{-1})		T_h (h)	
			Mean ± SE	95% CI	Mean ± SE	95% CI
19	II	0.67	0.13 ± 0.03	0.07–0.18	0.39 ± 0.03	0.34–0.45
23	II	0.26	0.31 ± 0.11	0.08–0.53	0.36 ± 0.02	0.32–0.41
27	II	0.74	0.35 ± 0.09	0.16–0.54	0.24 ± 0.01	0.21–0.27

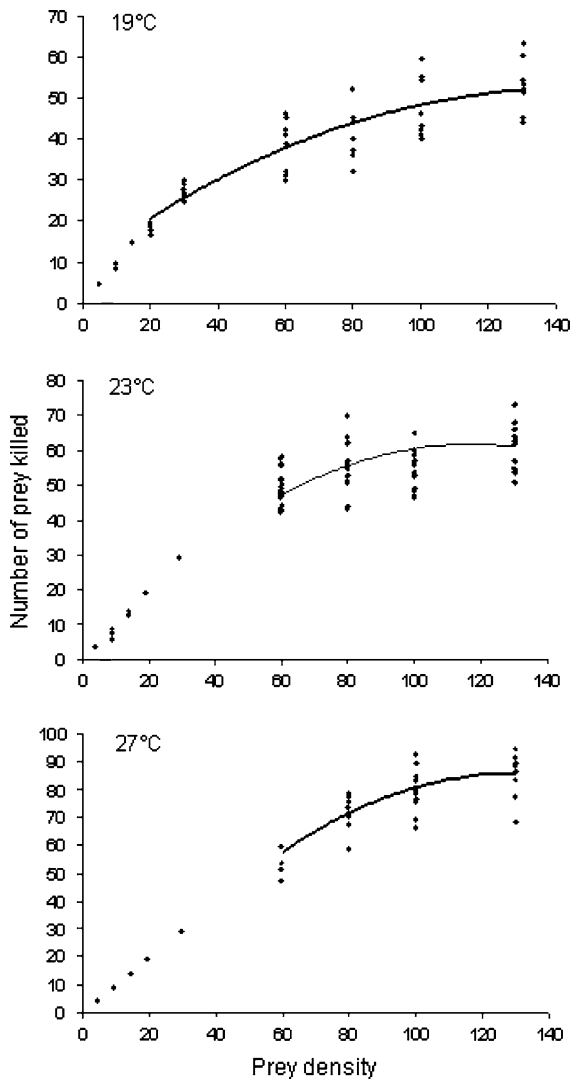*a* attack rate (on a 20–25 cm² leaf area), T_h handling time

Fig. 1 Observed numbers of *M. persicae* 3rd–4th instars killed in 24 h by *A. bipunctata* females versus numbers predicted by the random predator equation (lines) at three different temperatures on a 20–25 cm² leaf area. Lines were only drawn through densities included in the analysis (i.e., those without complete prey depletion)

Discussion

Juliano (2001) and Tully et al. (2005) reviewed experimental circumstances that violate the basic assumptions of Holling's (1959) disc equation, which is the most frequently used equation to model functional responses of predatory arthropods. One of the most common violations is prey depletion during the experiment. When killed prey are not replaced during exposure to the predator, Rogers'

(1972) model can be used as it accounts for changing prey densities. However, this model cannot correct for complete prey depletion before the end of the experiment. When all prey are eaten within the observation interval, no valid information can be derived from the experiment and including these densities in the analysis may yield biased estimates. Therefore, lower prey densities where prey were completely depleted by the end of the experiment were removed from the functional response analysis in the present study. Ideally, either the arena size should be increased or prey should be replenished at shorter time intervals in order to avoid complete prey depletion at lower initial densities of prey.

Between 19°C and 27°C, the rate of predation by adult females of *A. bipunctata* on 3rd and 4th instars of *M. persicae* increased with increasing prey density, but the mean ratio of prey killed decreased monotonically, suggesting a type II functional response (Holling 1959, 1965; Gotelli 1995). A similar response curve was reported earlier by Mills (1982) for *A. bipunctata* preying on *A. pisum* at 20°C. Type II functional response curves have been reported in a number of other coccinellids (Uygun and Atlihan 2000; Omkar and Pervez 2003; Lee and Kang 2004; Pervez and Omkar 2005; Mandour et al. 2006; Moura et al. 2006). However, type III functional responses have been also reported for coccinellids (Hu et al. 1989; Messina and Hanks 1998; Sarmento et al. 2007).

Some authors have challenged the efficacy of predators showing type II functional responses as biological control agents. Holling (1965) stated that predators showing a type III response are theoretically more capable of suppressing prey populations. Although the shape of the functional response curve is an important factor, it is insufficient as a criterion to predict success or failure of a predator as a biocontrol agent, as other factors such as numerical response, intrinsic growth rates, host patchiness, competition, and environmental complexities (abiotic and biotic factors) also have a major influence on the efficiency of a predator in managing a pest population (Pervez and Omkar 2005; see also below). A review by Fernández-arhex and Corley (2003) showed that most parasitoid species have a type II response, but there is no clear relationship between curve shape and biocontrol success in these insects. The form of the functional response curve may vary according to

environmental conditions (Abrams 1982), such as habitat heterogeneity (Hildrew and Townsend 1977; Kaiser 1983; Lipcius and Hines 1986), light intensity (Koski and Johnson 2002), host plant (Carter et al. 1984; Messina and Hanks 1998; De Clercq et al. 2000; Skirvin and Fenlon 2001), temperature (Thompson 1978; Gresens et al. 1982; Bailey 1989; Mohaghegh et al. 2001; Mahdian et al. 2006; Li et al. 2007) and refuge for prey (Lipcius and Hines 1986; Messina and Hanks 1998). In the current study, temperature clearly influenced the magnitude of predator response to prey density (Fig. 1). This may be attributed to temperature-related changes in the metabolism and activity of predator and prey (McCoull et al. 1998). Higher temperatures increased the functional response of *A. bipunctata* by increasing attack rate and decreasing handling time. Similar observations were reported by Thompson (1978), Gresens et al. (1982), Bailey (1989), Anderson et al. (2001) and Gotoh et al. (2004). Our findings suggest that *A. bipunctata* spent more time in non-searching activities (e.g., resting) at low temperatures (19°C), while more intensive searching and feeding occurred at higher temperatures (above 23°C).

The current study suggests that an individual *A. bipunctata* female can kill a theoretical maximum number of 61, 67 and 100 3rd–4th instars of *M. persicae* per day at 19, 23 and 27°C, respectively. These numbers are higher than those reported by Chi and Yang (2003) for *Propylea japonica* Thunberg and Cabral et al. (2006) for *Coccinella undecimpunctata* L. preying on *M. persicae*. However, comparison of the predation rates of *A. bipunctata* in our study with those of other coccinellids is complicated by variability in the size of predators and prey and in experimental conditions (e.g., test arena, temperature).

Functional responses may provide important information on the voracity of a biological control agent, and on the effects of abiotic (e.g., temperature) or biotic (e.g., host plants) factors on its foraging efficiency (e.g., Carter et al. 1984; Messina and Hanks 1998; De Clercq et al. 2000; Mohaghegh et al. 2001; Skirvin and Fenlon 2001; Mahdian et al. 2006; Li et al. 2007). However, functional response studies have been criticized because they are often performed in small artificial arenas using unrealistic prey densities and do not consider spatial habitat complexities or multispecies prey situations (van Lenteren and Bakker 1976; Murdoch 1983; O'Neil 1989,

1997; Kareiva 1990; Wiedenmann and O'Neil 1991; Messina and Hanks 1998; Hardman et al. 1999). Furthermore, functional responses do not consider crucial life history parameters of a predator that may affect its value as a biological control agent. In the case of coccinellid predators, the selection of prey patches by female adults is determined by expectations of future bottlenecks in prey abundance (Dixon 2000). Many aphidophagous predators have evolved the ability to attack prey colonies at an early stage of development to maximize the fitness of their offspring. Dixon (2000) proposed that the most important attribute of an effective biological control agent is the rate of its development relative to that of its prey, i.e., the generation time ratio. According to this hypothesis, if the developmental rate of a predator is similar to or faster than that of the prey then the predator is potentially capable of suppressing the prey population. This concept would render *A. bipunctata* and other aphidophagous coccinellids ineffective biological control agents, given the high intrinsic rates of increase of most aphid species (Dixon 2000). However, advanced larval stages are released in relatively high numbers in many augmentative biological control programmes using aphidophagous coccinellids (e.g., Ferran et al. 1998; Wyss et al. 1999a, b). Commercial packagings of *A. bipunctata* usually contain second to third instars (J. Vermeulen, BioBest NV, personal communication). In such an inundative approach the objective is short term pest suppression by the released larvae and the resulting adults rather than long term control of the aphid populations. In addition, *A. bipunctata* larvae can be released in aphid hot spots rather than in the whole crop.

The current study shows that *A. bipunctata* displays relatively high predation rates on *M. persicae* at a wide range of temperatures, indicating its potential for augmentative releases against the green peach aphid. Functional response models have served as a basis for developing ecological theory on foraging behavior and tritrophic interactions between plants, prey and predators (or parasitoids) (Holling 1959; Hassell 1978; Messina and Hanks 1998; Tully et al. 2005). Measures of voracity from functional response experiments may be indicative of the value of coccinellid predators as augmentative biological control agents and provide a basis for determining release rates appropriate for various aphid densities.

However, robust experimental assessment of functional responses remains difficult and certain behavioral responses that are crucial in a biological control context cannot be taken into account in the experimental design (van Lenteren and Bakker 1976, 1978; Tully et al. 2005). For instance, laboratory studies may indicate the predation potential of *A. bipunctata* when aphids are abundant, but they do not consider cannibalism or emigration of the predator that may occur when aphid populations start to decline, leaving few predators in the crop in case the aphids would resurge. Therefore, more field studies are needed to understand the foraging behavior of *A. bipunctata* in different cropping systems, in order to design practical release strategies for this coccinellid.

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