

Effects of temperature on predation by the stinkbugs *Picromerus bidens* and *Podisus maculiventris* (Heteroptera: Pentatomidae) on noctuid caterpillars

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Abstract

Environmental risks associated with the use of non-indigenous organisms for augmentative biological control have received growing attention. In Europe, the native pentatomid predator *Picromerus bidens* (Linnaeus) has been considered a potential alternative to the North American pentatomid *Podisus maculiventris* (Say) for the control of lepidopteran, coleopteran and hymenopteran defoliator pests. In the current study, prey consumption and developmental duration of the predatory stages of *P. bidens* and *P. maculiventris* were investigated at three temperatures (18, 23 and 27°C) in the laboratory using caterpillars of *Spodoptera littoralis* as prey. Development time from second to fifth instar was longer for *P. bidens* than for *P. maculiventris*, taking on average 17–44 and 14–32 days, respectively, at the different temperatures. Total nymphal consumption of fourth instar *S. littoralis* caterpillars indicated a greater voracity of *P. bidens* as compared with *P. maculiventris* at both the low and high temperatures tested (18 and 27°C). At 23°C, however, the predation rate of *P. maculiventris* nymphs exceeded that of *P. bidens* nymphs. Effect of temperature on the functional response of *P. bidens* to densities of fourth instar *Spodoptera exigua* was assessed on potted green bean plants. Female adults of *P. bidens* exhibited a type II functional response at 18 and 23°C but a type III response at 27°C. Searching efficiency was not affected by temperature but handling time decreased from 4.2 to 1.4 h as temperature increased from 18 to 23°C. However, the predator spent twice as much time handling prey at 27°C (2.9 h) than at 23°C. This study indicates high predation rates of *P. bidens* at a wide range of temperatures and suggests that the species may be a valuable asset for the biological control of defoliating caterpillars, provided that obstacles to its mass production can be overcome.

Keywords: *Picromerus bidens*, *Podisus maculiventris*, *Spodoptera exigua*, *Spodoptera littoralis*, functional response, temperature, biological control

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Introduction

Increasing concerns about potential non-target effects of exotic biological control agents on the indigenous fauna have been expressed during the last decade. Some risks and concerns related to the introduction and use of invertebrate biological control agents have been reviewed by De Clercq (2002) and van Lenteren *et al.* (2003).

Podisus maculiventris (Say), a common generalist predator found throughout North America reportedly feeds on a wide range of insect prey, mainly soft-bodied lepidopterous and coleopterous larvae (McPherson, 1980, 1982; De Clercq, 2000). This predator was first introduced in Europe in the 1930s for control of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) and has been used commercially in European greenhouses since 1997 to suppress caterpillar outbreaks (Couturier, 1938; De Clercq, 2000). van Lenteren *et al.* (2003) developed a procedure for environmental risk assessment of non-indigenous natural enemies used in augmentative biological control in Europe and, largely based on literature reviews, *P. maculiventris* was one of the exotic natural enemies which were attributed a high risk index. As a result, the use of this American species for biological control in Europe was greatly criticized.

Picromerus bidens (Linnaeus) is another predatory pentatomid that is naturally distributed from North Europe into China and North Africa and also occurs in parts of North America after its inadvertent introduction sometime before 1932 (see De Clercq, 2000, for references). Given its extensive geographical range, this predator is locally adapted to a variety of climates. It is associated with a wide variety of plants, including herbaceous plants, shrubs (e.g. raspberries) and a multitude of deciduous and coniferous trees. The predator feeds mainly on larval forms of more than 250 insect species, including economically important defoliator pests of the Lepidoptera (e.g. Noctuidae, Geometridae, Lymantriidae, Pieridae), Coleoptera (e.g. Chrysomelidae) and Hymenoptera (e.g. Diprionidae, Tenthredinidae) (Javahery, 1986; Larivière & Larochelle, 1989). Although some studies have reported on the capacity of *P. bidens* to reduce populations of insect pests (e.g. Gäbler, 1937, 1938; Engel, 1939; Clausen, 1940; Forsslund, 1946; Pschorn-Walcher & Zinnert, 1971; Mallach, 1974; Volkov & Tkacheva, 1997), the potential of this predator for augmentative biological control is largely unknown.

As predation behaviour of an arthropod predator may be affected by temperature, this laboratory study compares predation rates of *P. maculiventris* and *P. bidens* at different constant temperatures, using caterpillars of the cotton leafworm, *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae) as prey. The cotton leafworm is a major polyphagous pest with a wide distribution throughout Africa, the Mediterranean region, and several parts of Asia (Sneh *et al.*, 1981; Kumar & Ballal, 1992). This noctuid is among the most destructive lepidopterous crop pests within its subtropical and tropical range, and has the potential to become a pest of glasshouse crops in northern Europe.

In addition, this study investigates functional response of *P. bidens* to densities of another noctuid pest, *Spodoptera exigua* (Hübner), as a function of temperature. The beet armyworm, *S. exigua*, is an economically important pest in numerous crops worldwide and originates from Southeast Asia (East *et al.*, 1989). In northern Europe, the beet armyworm sporadically infests glasshouse cultures and has

been reported to cause considerable damage to a variety of vegetable and ornamental crops (De Clercq & Degheele, 1994; van der Linden, 1996).

Providing more insight into the predator-prey interactions of *P. bidens* is essential for the development of efficient biological control programmes targeting noctuid defoliators and using this native European predator as a possible alternative to *P. maculiventris*.

Materials and methods

Insects

A laboratory colony of *P. maculiventris* was established in 1999 with individuals collected from a field near Beltsville, Maryland. Predators used in the experiments were in the 42nd generation of laboratory rearing. A culture of *P. bidens* was started with eggs supplied by the Department of Entomology and Biological Control, All-Russian Research Institute for Plant Quarantine, Moscow, Russia. *Picromerus bidens* used in this experiment was in the fifth generation of laboratory rearing. The diet of stock colonies of both predators consisted mainly of larvae of the greater wax moth, *Galleria mellonella* (Linnaeus). Wax moth larvae were reared on an artificial diet modified from Vanhaecke & Degheele (1980). Cotton leafworms, *S. littoralis*, and beet armyworms, *S. exigua*, were occasionally also supplied as food in predator cultures. Both noctuid species were reared on an artificial diet that was modified from Poitout & Bues (1970).

Prey consumption

Prey consumption of the different predatory stages of both species was studied at three constant temperatures (18, 23, 27±1°C) using fourth instars of *S. littoralis* as prey. Predation by nymphs was only quantified from the second instar onwards (the first instars are not predaceous), and for adults, both males and females were tested. Relative humidity was maintained at 65±5% and the photoperiod for the experiment was 12:12 (L:D)h. Short-day conditions were chosen because long days induce reproductive diapause in females of *P. bidens* (Musolin & Saulich, 2000). Predator nymphs of each instar were newly moulted and unfed (<12h old), adults were reproductively active and were starved for 24h before testing. Nymphs and adults of both predators were confined in triple-vented plastic Petri dishes (9cm diameter, 1.5cm high) lined with absorbent paper. Moisture was supplied by way of a moist paper plug fitted into a plastic cup (2.5cm in diameter). Cubes of artificial diet were provided in excess as food for prey caterpillars. Twenty replicates were used for each predator-prey combination. Second, third, fourth and fifth instars, and male and female adults were offered 3, 4, 5, 7, 15, and 15 fourth instars of *S. littoralis* per day, respectively. Predation by nymphs was monitored daily throughout development and dead prey were replaced to keep prey density constant. Developmental duration of the nymphs was also recorded. Predation by male and female adults of *P. maculiventris* and *P. bidens* predators was recorded after 24h. Predation rates were compared among species at each temperature using Student's *t*-test and within a species, developmental duration of nymphs and predation rate of the different life stages

as a function of temperature were analysed using analysis of variance (ANOVA) and Tukey's test ($P=0.05$).

Functional response

The functional response of female adults of *P. bidens* to the density of fourth instars of *S. exigua* was measured in the laboratory at three temperatures (18, 23 and $27 \pm 1^\circ\text{C}$). The experiments were performed in acrylic plastic cylinders (25 cm high, 17 cm diameter), the top of which was covered with fine mesh screen. Each cylinder contained a single potted green bean plant, *Phaseolus vulgaris* cv. Prelude. Bean plants were 20–25 cm tall, with an average leaf area of 850–900 cm². Beet armyworms were fed on green bean foliage before being used as prey in the experiments in order to allow them to adapt to the food plant. Six densities of fourth-instar beet armyworms (17.8 ± 4.3 mg, $n=30$) were used: 1, 2, 4, 8, 16 and 24 individuals per plant arena. To standardize predator response, each female was starved for 24 h before testing. Both prey and predator were allowed 1 h for acclimation at each temperature before starting the experiment. Prey were distributed over the bean plants to obtain the required density and a single female predator (3 to 4 weeks old) was introduced into each cylinder. The experiments were conducted in growth chambers set at the respective temperatures, a relative humidity of $65 \pm 5\%$ and a photoperiod of 12:12 (L:D)h. The experiments were replicated 9 times simultaneously and controls (consisting of arenas without a predator) were used for each density. Killed prey were not replaced during the experimental period. After 24 h, the total number of live and dead prey was counted.

Functional responses of types II and III have received a great deal of attention in the entomological and ecological literature (Juliano, 2001). The type II functional response is described by Holling's (1959) disk equation:

$$N_e = \frac{aN_T}{1 + aN_T}$$

where N_e is the number of prey eaten, a is the attack constant, N is prey density, T is the total time available, and T_h is the handling time per prey. In the type III functional response model, attack rate (a) is a function of initial prey density:

$$a = \frac{d + bN}{1 + cN}$$

where b , c and d are constants that must be estimated.

The functional responses of *P. bidens* were analysed using the SAS statistical package (SAS Institute, 1989). Model selection (i.e. type II or type III) involves using a logistic regression of the proportion of prey killed and prey density to determine the shape of functional response:

$$N_e/N_0 = \frac{\exp(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3)}{1 + \exp(P_0 + P_1N_0 + P_2N_0^2 + P_3N_0^3)}$$

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 parameters to be estimated. These parameters can be estimated by using the CATMOD procedure using a SAS program given by Juliano (2001). Significant negative or positive reactive linear coefficients in the expression fit to data on the proportion

of prey eaten N_e versus initial density N_0 , indicate type II or type III responses, respectively.

A non-linear least squares regression of number of prey eaten versus number offered was used to estimate and compare parameters of functional responses using the NLIN procedure in SAS. Functional response data were fitted to the random predator equation (Juliano, 2001). This equation accounts for prey depletion without replenishment of prey during the experiment (Rogers, 1972). This equation can be written for type II functional responses as follows:

$$N_e = N_0\{1 - \exp[a(T_h N_e - T)]\}$$

where a is the attack constant (instantaneous search rate), T_h is handling time and T is the total time available.

For type III functional responses, where a is a function of initial density, the equation can be written as:

$$N_e = N_0 \left\{ 1 - \exp \left[\frac{(d + bN_0)(T_h N_e - T)}{(1 + cN_0)} \right] \right\}$$

where b , c , and d are constants.

Results

Developmental duration of *P. bidens* and *P. maculiventris* fed on fourth instars of *S. littoralis* decreased with increasing temperature (table 1). Duration from second to fifth instar of both predators was significantly affected by temperature (*P. bidens*: $F=154.97$, $df=2$, $P<0.001$; *P. maculiventris*: $F=1056.98$, $df=2$, $P<0.001$). Development time from second to fifth instar was longer for *P. bidens* than for *P. maculiventris*, taking on average 17–44 and 14–32 days for the respective species at the different temperatures.

Predation rates of nymphs and adults of *P. bidens* and *P. maculiventris* on fourth instars of *S. littoralis* are reported in table 1. Results indicated that all nymphal stadia of both predators from the second instar onward were able to prey successfully on fourth-instar *S. littoralis*. In each nymphal stadium of *P. bidens* and *P. maculiventris* the mean number of *S. littoralis* larvae killed was significantly ($P<0.05$) affected by temperature and predation rate generally decreased with increasing temperature. Overall, mean prey consumption from second to fifth instar of both predators decreased from 18 to 27°C (*P. bidens*: $F=22.26$, $df=2$, $P<0.001$; *P. maculiventris*: $F=21.12$, $df=2$, $P<0.001$). Throughout development from second to fifth instar, nymphs of *P. bidens* killed on average 48 and 34 fourth-instar *S. littoralis* at 18 and 27°C , respectively, which was significantly more than nymphs of *P. maculiventris* consumed at these temperatures (38 and 25 fourth-instar *S. littoralis* at 18 and 27°C , respectively). At 23°C , however, total nymphal predation rate for *P. maculiventris* was significantly higher than that of *P. bidens*. Mean daily prey consumption of male and female adults of *P. bidens* and *P. maculiventris* was also influenced by temperature with greater predation rates at the higher temperature (27°C) (*P. bidens*, female: $F=15.10$, $df=2$, $P<0.001$, male: $F=7.52$, $df=2$, $P<0.002$; *P. maculiventris*, female: $F=19.20$, $df=2$, $P<0.001$, male: $F=16.46$, $df=2$, $P<0.001$). Daily prey consumption by female adults of *P. bidens* was greater than that by *P. maculiventris* females at 18 ($t=1.935$, $df=38$, $P=0.045$), 23 ($t=2.907$, $df=38$, $P=0.010$) and 27°C ($t=3.102$, $df=38$, $P=0.004$). There were no significant differences between consumption rates of male adults of *P. bidens* and *P. maculiventris* at 18 ($t=1.504$, $df=38$,

Table 1. Developmental duration and predation of nymphs, and predation by female and male adults of *Picromerus bidens* and *Podisus maculiventris* at three different temperatures (18, 23, 27°C) on fourth instars of *Spodoptera littoralis*.

Stage	Temperature (°C)	<i>Picromerus bidens</i>		<i>Podisus maculiventris</i>	
		Duration (days)	Predation rate ^a	Duration (days)	Predation rate ^a
Second instar	18	12.2±0.3 a	5.0±0.5 a A	6.9±0.2 a	7.7±0.4 a B
	23	5.1±0.1 b	4.4±0.2 ab A	4.0±0.0 b	5.8±0.4 b B
	27	4.1±0.1 c	3.6±0.2 b A	2.9±0.1 c	2.6±0.2 c A
Third instar	18	10.4±0.1 a	8.0±0.5 a A	7.0±0.0 a	7.7±0.5 a A
	23	5.5±0.1 b	6.2±0.7 b A	3.9±0.1 b	4.9±0.3 b B
	27	3.2±0.1 c	4.3±0.4 c A	3.0±0.1 c	3.7±0.3 b B
Fourth instar	18	10.4±0.1 a	12.5±0.7 a A	7.7±0.1 a	9.2±0.5 a B
	23	6.3±0.1 b	7.5±0.4 b A	4.0±0.0 b	6.2±0.4 b A
	27	3.5±0.2 c	9.2±0.9 b A	2.7±0.1 c	6.2±0.4 b B
Fifth instar	18	16.1±0.2 a	22.1±1.7 a A	12.9±0.1 a	17.3±1.1 a B
	23	7.5±0.1 b	13.4±0.8 b A	7.0±0.1 b	15.0±0.9 ab A
	27	6.1±0.6 c	13.6±0.9 b A	5.3±0.2 c	12.3±1.1 b B
Second-fifth instar	18	44.5±1.7 a	47.6±1.6 a A	32.5±0.3 a	38.2±1.2 a B
	23	24.5±0.3 b	31.4±1.1 b A	18.9±0.1 b	38.8±2.5 a B
	27	16.7±0.7 c	33.6±2.6 b A	13.6±0.4 c	24.9±1.3 b B
Adult female	18		8.0±1.2 a A		5.3±0.6 a B
	23		12.0±0.5 b A		9.0±0.3 b B
	27		13.5±0.3 b A		11.4±0.6 b B
Adult male	18		6.4±1.0 a A		4.6±0.5 a A
	23		8.0±1.1 a A		6.7±0.8 a A
	27		11.3±0.5 b A		9.6±0.4 b B

^a Means ± SE (N = 20); predation rate is expressed for nymphs as the number of prey killed during the total stadium and for adults as the number of prey killed per day.

Means within a column and in the same stage followed by the same lowercase letter (a, b, c) are not significantly different (Tukey's test, $P > 0.05$).

Means within a row followed by the same uppercase letter (A, B) are not significantly different (t -test, $P > 0.05$).

$P = 0.144$) and 23°C ($t = 0.981$, $df = 38$, $P = 0.335$) but predation rate of *P. bidens* males was significantly greater than that of *P. maculiventris* males at 27°C ($t = 2.384$, $df = 38$, $P = 0.024$).

In the functional response experiments, survival of fourth instars of *S. exigua* was high (>97%) in the controls at the three temperatures tested (χ^2 -test; $df = 59$, $P > 0.999$ in each case). Therefore, control mortality was considered negligible. Functional response curves of female adults of *P. bidens* to the various densities of fourth-instar larvae of *S. exigua* at different temperatures are depicted in fig. 1. The mean number of prey killed per day by *P. bidens* females ranged from 0.44 at a density of one prey and 18°C to 7.9 at a density of 24 prey and 27°C.

Logistic regression analyses indicated that the type of functional response shown by *P. bidens* females changed as a function of temperature (table 2). The negative sign of the estimates of the linear coefficients suggested a type II functional response at 18 and 23°C. A type III functional response is suggested by the outcome of the logistic regression at 27°C, with a positive estimate of the linear coefficient. Fitting a type II functional response at this temperature resulted in parameter estimates of $a = 0.074 \pm 0.030 \text{ h}^{-1}$ and $T_{1/2} = 2.29 \pm 0.45 \text{ h}$. Both parameters were significantly different from zero. However, the residual sum of squares for the type II model (275.5) exceeded that for the minimal type III model (266.9), indicating that a type III functional response fits the data better than a type II response. Estimates of the linear coefficient were not significantly different from zero

($P > 0.05$) at 18 and 27°C, suggesting that the data should be interpreted with caution. Juliano (2001) stated that at the model selection stage, significance testing is not as important as is obtaining a good description of the relationship of the proportion of prey eaten versus initial number of prey. In the current study the shapes of the curves of the proportion of prey eaten versus initial prey density confirmed the designated types of functional responses.

The relationships between temperatures, handling times and attack rates are shown in table 3. The data again show that the functional responses of female adults of *P. bidens* were highly affected by temperature. Based on asymptotic 95% confidence intervals, the attack rates of *P. bidens* were similar at 18 and 23°C, but handling times differed significantly among temperatures. Estimated handling times averaged 4.2, 1.4 and 2.9 h at 18, 23 and 27°C, respectively. The estimated attack coefficients averaged 0.019 h^{-1} at 18 and 23°C. The coefficients of determination (r^2) indicated greater variation in predation at 18°C than at 23 and 27°C.

Non-linear regression results at 27°C showed that the parameters c and d were not significantly different from zero. The reduced type III model at 27°C indicated that the relationship of attack rate a to initial prey density N was linear with a slope (b) of 0.016. Maximum predation rate (i.e. asymptotic maximum number of prey eaten per unit time) was estimated to be 5.6, 16.8 and 8.1 fourth instars of *S. exigua* per day at 18, 23 and 27°C, respectively.

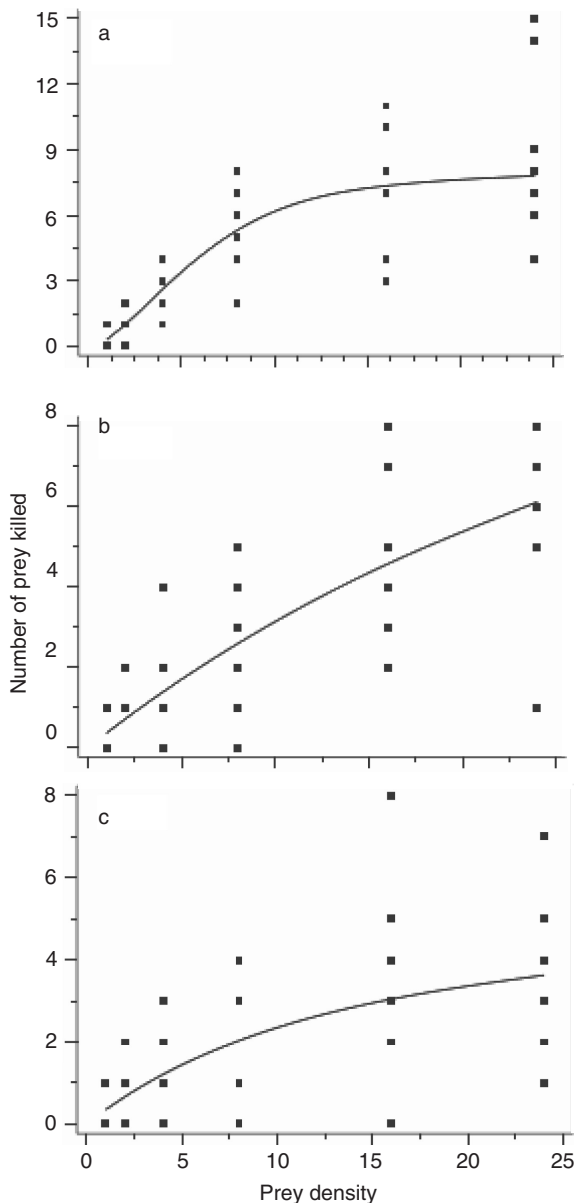


Fig. 1. Observed numbers of *Spodoptera exigua* fourth instars killed by *Picromerus bidens* females versus numbers predicted by the random predator equation (lines) at (a) 27°C, (b) 23°C and (c) 18°C.

Discussion

Total nymphal consumption of *S. littoralis* caterpillars indicated a greater voracity of *P. bidens* compared with *P. maculiventris* at both the low and high temperature tested (18 and 27°C). At 23°C, however, predation rate of *P. maculiventris* nymphs exceeded that of *P. bidens* nymphs. Predation rates of nymphs are in part determined by developmental period, which may result in greater total predation rates at lower temperatures. As temperature increases, developmental period decreases, but the shorter time available for attacking prey is partly compensated by

greater predator activity. Predation rates of female adults of *P. bidens* on *S. littoralis* fourth instars were superior to those of *P. maculiventris* females at each temperature tested, despite similar body weights (averaging 100–120 mg for newly emerged female adults of either pentatomid species, Mahdian *et al.* (2006)).

Functional response is a key component in the selection of predators and parasitoids for biological control and it can also be a useful tool when investigating the impact of environment on the effectiveness of natural enemies (Juliano, 2001). Temperature has been recognized as one of the most important physical factors in the dynamics of arthropod predator–prey or parasitoid–host interactions and as a consequence the type of functional response may be affected by it. A change in response may be the result of changes in the foraging behaviour as temperature varies. Differential searching responses as a function of temperature have been documented for various arthropod natural enemies (e.g. Zhang *et al.*, 1983; Enkegaard, 1994; Song & Heong, 1997; Wang & Ferro, 1998; Mohaghegh *et al.*, 2001; Skirvin & Fenlon, 2003; Gilioli *et al.*, 2005; Kalyebi *et al.*, 2005).

Laboratory and field experiments have indicated different types of functional responses in Asopinae (De Clercq, 2000). In a number of studies, *P. maculiventris* has shown type II (Morris, 1963; Mukerji & LeRoux, 1969; Waddill & Shepard, 1975; O'Neil, 1989, 1997; Wiedenmann & O'Neil, 1991; De Clercq *et al.*, 1998; Mohaghegh *et al.*, 2001) or type III responses (Mohaghegh *et al.*, 2001). In the current study, female adults of *P. bidens* exhibited a type II functional response at 18 and 23°C but a type III response at 27°C. Likewise, *P. maculiventris* and the Neotropical species *Podisus nigrispinus* (Dallas) had a type II response at 18°C and a type III response at 27°C (Mohaghegh *et al.*, 2001). The type III response observed at higher temperatures indicates that prey capture is relatively poor at low prey densities and increases with an accelerating search rate as the predator encounters increasing densities of prey. In laboratory studies using relatively small arenas, a shift from a type II response to a type III response may result from an increased physical activity of the predator at higher temperature in a constrained environment.

The effect of temperature on functional response can further be explained by the parameter estimates of attack rate a and handling time T_h . Whereas attack rate was not affected by temperature, handling time (i.e. the time needed for attacking, killing and consuming prey plus the time spent resting or plant feeding after a successful attack (De Clercq *et al.*, 2000)) decreased from 4.2 to 1.4 h as temperature increased from 18 to 23°C. However, the predator spent twice as much time handling prey at 27°C (2.9 h) than at 23°C. Increased handling time at 27°C may be explained in part by greater mobility and more aggressive defence of the *S. exigua* caterpillars or by a reduction of predator searching activity at this temperature. To confirm this, further studies examining the searching and attacking behaviour of *P. bidens* in more detail are required. Handling times estimated in the current study for *P. bidens* females preying on fourth instars of *S. exigua* are shorter than those reported by Mohaghegh *et al.* (2001) for *P. maculiventris* females feeding on the same prey at 23°C (1.4 versus 2.6 h, respectively) but somewhat longer at 18°C (4.2 versus 3.1 h) and 27°C (2.9 versus 2.3 h). It is worth noting, however, that the experiments of Mohaghegh *et al.* (2001) were carried out under long day conditions (16 h photoperiod) using sweet pepper plants,

Table 2. Maximum-likelihood estimates from logistic regressions of the proportion of *Spodoptera exigua* fourth instars eaten by *Picromerus bidens* on initial prey density at different temperatures.

Temperature (°C)	Coefficient	Estimate	SE	χ^2	P
18	Constant (p_0)	0.2924	0.6052	0.23	0.6290
	Linear (p_1)	-0.3664	0.2095	3.06	0.0804
	Quadratic (p_2)	0.0258	0.0183	2.00	0.1578
	Cubic (p_3)	-0.00059	0.000445	1.73	0.1881
23	Constant (p_0)	1.6891	0.6318	7.15	0.0075
	Linear (p_1)	-0.6962	0.2121	10.78	0.0010
	Quadratic (p_2)	0.0522	0.0181	8.35	0.0039
	Cubic (p_3)	-0.00117	0.000434	7.24	0.0071
27	Constant (p_0)	-0.3694	0.5855	0.40	0.5281
	Linear (p_1)	0.3523	0.1940	3.30	0.0963
	Quadratic (p_2)	-0.0335	0.0165	4.10	0.0430
	Cubic (p_3)	0.000757	0.000397	3.63	0.0566

Table 3. Parameters (means \pm SE) estimated by the random predator equation, indicating functional response of *Picromerus bidens* females to densities of *Spodoptera exigua* fourth instars at different temperatures.

Temperature (°C)	Type	a (h^{-1})	b	T_h (h)	r^2
18	II	0.019 ± 0.008	-	4.25 ± 1.15	0.40
23	II	0.019 ± 0.005	-	1.43 ± 0.85	0.63
27	III	^a	0.016 ± 0.007	2.95 ± 0.26	0.64

^a In the best fit type III model, relationship between attack rate and initial number of prey is linear ($a = bN$).

whereas in the current study short day conditions (12h photoperiod) and green bean plants were used. Finally, handling times estimated by the functional response equations should not be considered as absolute calculations of the predator's time budget. Several studies have indicated differences between model-estimated handling times and those obtained from direct observations (De Clercq *et al.*, 2000).

In a laboratory environment, *P. bidens* has demonstrated high predation capacities against noctuid caterpillars within a wide range of temperatures. The performance of this Palearctic species compares well to that of the Nearctic pentatomid *P. maculiventris*, a species with a widely recognized biocontrol potential (De Clercq, 2000). *Picromerus bidens* may thus have potential for augmentative release in biological control programmes targeting lepidopteran defoliators. In Europe, it may be an alternative to the North American species *P. maculiventris*, the use of which has largely been abandoned as a result of growing environmental concerns based on its wide host range and establishment potential (van Lenteren *et al.*, 2003). Predation rates of *P. bidens* observed at relatively low (18°C) and high temperatures (27°C) suggest that the predator may perform well both in open fields of temperate climates and in heated glasshouses. Moreover, given its extensive geographic range, it may be rewarding to search for strains that are adapted to different temperature regimes for use in augmentative biocontrol programmes in various climates and agricultural settings. However, the traits that determine the potential of a predator as a biocontrol agent are not only related to pest

suppression. Cheap and reliable mass production is a prerequisite for cost-effective biological control (De Clercq, 2004). *Podisus maculiventris* is easily reared on a variety of natural and unnatural foods and is a prolific egg layer, with reported fecundities of over 1000 eggs per female (De Clercq, 2000). In contrast, mass production of *P. bidens* may be hampered by its limited nutritional plasticity (complicating the use of factitious foods or artificial diets), low reproductive capacity (with a lifetime fecundity of 100–200 eggs per female), and obligatory egg diapause (Musolin & Saulich, 2000; Mahdian *et al.*, 2006). Finally, predation rates observed in the laboratory cannot simply be extrapolated to the field situation and field experiments are needed to more accurately predict the value of *P. bidens* as a biocontrol agent. Field experiments are currently being done in a number of European countries (including The Netherlands, Germany and Russia) to investigate the potential of *P. bidens* to suppress outbreaks of lepidopteran, coleopteran and hymenopteran defoliators in various agroecosystems.

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