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19

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

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25

26 **Abstract**

27 The effect of temperature on the functional response of female adults of the two-spot ladybird,
28 *Adalia bipunctata* L. (Coleoptera: Coccinellidae) was examined in petri dish arenas containing
29 sweet pepper leaves infested with different densities of the green peach aphid, *Myzus persicae*
30 (Sulzer) (Hemiptera: Aphididae). The predator showed a type II functional response at three
31 tested temperatures ranging from 19 to 27°C. The theoretical maximum number of prey
32 captured by the predator increased with temperature. Based on the random predator equation,
33 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
34 cm². There was no significant difference between the attack rates of the predator at 23 and
35 27°C. Handling time significantly decreased as temperature increased from 19 (0.39 h) to 27°C
36 (0.24 h). This study shows that *A. bipunctata* displays high predation rates on *M. persicae* for a
37 wide range of temperatures, indicating its potential for augmentative releases against this aphid
38 pest. The limitations of the predictions generated by functional response experiments are
39 discussed.

40

41 **Keywords** *Adalia bipunctata*, *Myzus persicae*, Coccinellidae, Aphididae, functional response,
42 predation, augmentative biological control

43

44 **Running head:** Functional response of *Adalia bipunctata* on *Myzus persicae*

45

46 **Introduction**

47

48 A quantitative and qualitative understanding of the interaction among different species is crucial
49 for the management of agricultural pests. Each species in an agricultural ecosystem is part of an
50 often complex community, where it has to interact with many other species. These interactions
51 may be competitive, predatory, parasitic or mutualistic (Begon et al. 1996; Bellows and Hassell
52 1999). One of the most important interactions with implications for biological control is the
53 predator-prey relationship. How predators respond to changes in prey availability (i.e. functional
54 response) is an issue of particular interest (Jeschke et al. 2002) and can determine whether a
55 predator is able to regulate the density of its prey (Murdoch and Oaten 1975). The functional
56 response has traditionally been defined as the number of prey attacked by an individual natural
57 enemy in relation to host density over a given time interval (Solomon 1949). The response is
58 characterized by an increase in the number of prey (or hosts) attacked over the lower range of
59 prey densities, and an upper limit to the number of prey attacked at higher prey densities due to
60 satiation in the case of predators (Mills 1982; Jeschke et al. 2002) and egg limitation or handling
61 time constraints in the case of parasitoids (Getz & Mills 1996; Mills and Lacañ 2004). Basically,
62 functional responses have been delimited to three different types (Holling 1959). A type I
63 response is characterized by a linear increase, a type II response by a monotonic decelerating
64 increase, and a type III response by a sigmoidal increase in host numbers attacked. The type II
65 functional response is the most frequently reported type in insects (Hassell et al. 1976; Begon et
66 al. 1996), including coccinellids (Hodek and Honek 1996; Dixon 2000). However, predators may
67 show different types of functional response curves as a function of host plant (Messina and
68 Hanks 1998; De Clercq et al. 2000) or prey type (Sarmiento et al. 2007). *Harmonia axyridis*

69 (Pallas) has been reported to exhibit type I (Lou 1987), type II (He et al. 1994), and type III (Hu et
70 al. 1989) functional responses on different aphid species. Interestingly, third instars and adults
71 of *H. axyridis* exhibited different types of responses (type II and I, respectively) on the eggs of
72 the monarch butterfly, *Danaus plexippus* (L.) (Koch et al. 2003).

73 In order to model predation by a long-lived, polyphagous predator, it is essential to
74 know how the key parameters of the functional response (i.e. the attack coefficient, a , and
75 handling time, T_h) scale with temperature (Thompson 1978). However, there are few data
76 showing the influence of temperature on type and magnitude of the functional response of
77 coccinellid predators. Overall, the predation rate of larval and adult stages of coccinellids has
78 been reported to increase with temperature within a range of ca. 10-30 °C (Mack and Smilowitz
79 1982a,b; Giroux et al. 1995; Xia et al. 2003; Gotoh et al. 2004).

80 The two-spotted ladybird beetle, *Adalia bipunctata* (L.), is a common natural enemy of
81 aphids in Europe and Central Asia (Mills 1979; Majerus 1994) and has been considered a
82 potential biological control agent in different agro-ecosystems (Majerus 1994; Hodek and Honek
83 1996; Dixon 2000; Omkar and Pervez 2005). Although some studies have investigated the
84 functional response of *A. bipunctata* (Mills 1979, 1982; Hemptinne et al. 1996), none of them
85 have addressed the effect of temperature on the functional response of the predator. Mills
86 (1979, 1982) found that prey consumption by female adults of *A. bipunctata* increased
87 curvilinearly suggesting a type II functional response. On the contrary, the males of this species
88 were not found to show a functional response (Hemptinne et al. 1996).

89 The objective of the current study is to investigate the effects of temperature on the
90 functional response of *A. bipunctata* to different densities of the green peach aphid, *Myzus*
91 *persicae* (Sulzer). Improving our understanding of the predator-prey interactions between *A.*

92 *bipunctata* and *M. persicae* may be helpful to optimize biological control of this economically
93 important aphid pest.

94

95

96 **Materials and Methods**

97

98 Insects

99

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

108

109 Functional response experiment

110

111 The experiment was performed at three constant temperatures (19, 23 and $27 \pm 1^\circ\text{C}$), a relative
112 humidity of $65 \pm 5\%$ and a photoperiod of 16:8 (L:D) h. The selected temperatures should reflect
113 thermal conditions frequently experienced by the predator in different protected and field crops
114 in temperate areas. The female *A. bipunctata* used in the experiment had body weights ranging
115 from 12.1-13.4 mg. At each of the tested temperatures, females were used that had initiated
116 oviposition (i.e. 8-10 days old). To standardize the response, predators were starved for 24 h in
117 boxes containing only a source of moisture before release into the test arena. The experimental
118 arena consisted of a plastic Petri dish (14 cm in diameter) lined with paper towel. Each dish
119 contained a sweet pepper leaf with its petioles inserted into an Eppendorf tube (2ml) filled with
120 water. The average leaf area (both sides) was estimated to be approximately 20-25 cm² (n = 5
121 leaves). Third and fourth instars of *M. persicae* were used as prey in the experiment. Aphids
122 were gently transferred by a fine camel hair brush from plants of the stock culture to the leaves
123 in the test arenas. Prey densities used were: 5, 10, 15, 20, 30, 60, 80, 100 and 130 aphids per
124 leaf. The aphids were allowed to settle and a female adult predator was introduced in each Petri
125 dish. At each prey density, there were ten replicates for predator treatments and 5 controls (i.e.
126 arenas without a predator). The total number of prey killed during a 24-h period was recorded.
127 Killed prey were not replaced during the experiment (prey depletion method). Predation
128 mortality was corrected for control mortality using the formula given by Xia et al. (2003):

129
$$N_e = N_0 \frac{N_d - N_c}{N_0 - N_c} \quad (1),$$

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

133

134 Data analysis

135

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

140 Analysis of the functional response consists of two distinctive steps (De Clercq et al.
141 2000; Juliano 2001): determination of the type of functional response and estimation of the
142 parameters of the functional response curve. The shape of the functional response is
143 determined by a logistic regression of the proportion of prey eaten as a function of initial
144 density. This is done by fitting a polynomial function:

$$145 \frac{N_e}{N_0} = \frac{\exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)}{1 + \exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)} \quad (2),$$

146 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
147 the parameters to be estimated. To estimate these parameters, the CATMOD procedure was
148 used (Juliano 2001). The data sets were individually fitted to the model (2), for determining the
149 type of functional response (type II or III). The sign of P_1 and P_2 can be used to distinguish the
150 shape of the curves. A positive linear parameter (P_1) and a negative quadratic parameter (P_2)
151 indicate that the functional response is type III, whereas if both parameters are negative, the
152 functional response is type II (Juliano 2001). In the second step, a nonlinear least square
153 regression (NLIN) procedure was used to estimate the parameters of the random predator

154 equation (T_h and a for type II and b , c , and d for type III) (Rogers 1972; Juliano 2001). These
155 equations are described by:

156
$$N_e = N_0 \{1 - \exp[a(T_h N_e - T)]\}$$
 (type II, prey depletion) (3),

157
$$N_e = N_0 \{1 - \exp[(d + bN_0)(T_h N_e - T)/(1 + cN_0)]\}$$
 (type III, prey depletion) (4),

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

164

165

166 **Results**

167

168 The proportion of prey consumed by the predator declined with increasing prey density,
169 justifying the decision to use non-linear curve fitting (Table 1). The negative linear coefficient
170 ($P_1 < 0$) suggests that there was a type II functional response at all tested temperatures. Because
171 estimates of the linear coefficient in the original cubic model were not significantly different
172 from 0 ($P > 0.05$) in the case of 23°C and 27°C, the model was reduced by subsequently omitting
173 the cubic term until all remaining coefficients were significant (Juliano, 2001; Mahdian et al.,
174 2006). The negative sign of the estimates of the linear coefficient (P_1) in the reduced models for

175 23°C (quadratic model: $P_1 = -0.0884$, $P < 0.0001$) and 27°C (quadratic model: $P_1 = -0.0869$, $P <$
176 0.0001) confirmed the designated types of functional response in the original model. Significant
177 quadratic terms (P_2) were derived for *A. bipunctata* at temperatures ranging from 19°C and
178 23°C, indicating that asymptotically declining proportions of prey were killed by the predator at
179 these temperatures.

180 All data were fitted to the random predator equation. The coefficients of determination
181 (R^2) indicated greater variation in predation rates at 23 °C than at 19 and 27°C (Table 2). The
182 number of *M. persicae* nymphs killed by *A. bipunctata* females increased at a decreasing rate
183 until reaching an upper plateau, as the number of *M. persicae* offered increased (Fig. 1). The
184 theoretical maximum number of prey captured by the predator increased with temperature. A
185 two-way ANOVA with prey density and temperature as factors revealed a significant difference
186 in predation at the different prey densities ($F_{8,243} = 878.90$, $P < 0.001$) and across temperatures
187 ($F_{2,243} = 185.54$, $P < 0.001$). The interaction between the two factors was also significant ($F_{16,243} =$
188 30.54, $P < 0.001$).

189 The relationship between temperature, handling times and attack rates, calculated from
190 the response curves, is shown in Table 2. Handling time significantly decreased ($F_{2,29} = 344.083$, P
191 < 0.001) as temperature increased from 19 (0.39h) to 27°C (0.24h). Likewise, there was a
192 significant effect of temperature on attack rate ($F_{2,29} = 26.414$, $P < 0.001$). Attack rate on a 20-25
193 cm² leaf area at 23°C (0.31 hour⁻¹) was higher than that at 19°C (0.13 hour⁻¹), but similar to that
194 at 27°C (0.35 hour⁻¹). The estimated maximum numbers of 3rd-4th instars of *M. persicae* that can
195 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
196 27°C, respectively.

197

198

199 **Discussion**

200

201 Juliano (2001) and Tully et al. (2005) reviewed experimental circumstances that violate the basic
202 assumptions of Holling's (1959) disc equation, which the most frequently used equation to
203 model functional responses of predatory arthropods. One of the most common violations is prey
204 depletion during the experiment. When killed prey are not replaced during exposure to the
205 predator, Rogers' (1972) model can be used as it accounts for changing prey densities. However,
206 this model cannot correct for complete prey depletion before the end of the experiment. When
207 all prey are eaten within the observation interval, no valid information can be derived from the
208 experiment and including these densities in the analysis may yield biased estimates. Therefore,
209 lower prey densities where prey were completely depleted by the end of the experiment were
210 removed from the functional response analysis in the present study. Ideally, either the arena
211 size should be increased or prey should be replenished at shorter time intervals in order to avoid
212 complete prey depletion at lower initial densities of prey.

213 Between 19 and 27°C, the rate of predation by adult females of *A. bipunctata* on 3rd and
214 4th instars of *M. persicae* increased with increasing prey density, but the mean ratio of prey
215 killed decreased monotonically, suggesting a type II functional response (Holling 1959, 1965;
216 Gotelli 1995). A similar response curve was reported earlier by Mills (1982) for *A. bipunctata*
217 preying on *A. pisum* at 20°C. Type II functional response curves have been reported in a number
218 of other coccinellids (Uygun and Atlihan 2000; Omkar and Pervez 2003; Lee and Kang 2004;
219 Pervez and Omkar 2005; Mandour et al. 2006; Moura et al. 2006). However, type III functional

220 responses have been also reported for coccinellids (Hu et al. 1989; Messina and Hanks 1998;
221 Sarmiento et al. 2007).

222 Some authors have challenged the efficacy of predators showing type II functional
223 responses as biological control agents. Holling (1965) stated that predators showing a type III
224 response are theoretically more capable of suppressing prey populations. Although the shape of
225 the functional response curve is an important factor, it is insufficient as a criterion to predict
226 success or failure of a predator as a biocontrol agent, as other factors such as numerical
227 response, intrinsic growth rates, host patchiness, competition, and environmental complexities
228 (abiotic and biotic factors) also have a major influence on the efficiency of a predator in
229 managing a pest population (Pervez and Omkar 2005; see also below). A review by Fernández-
230 arhex and Corley (2003) showed that most parasitoid species have a type II response, but there
231 is no clear relationship between curve shape and biocontrol success in these insects. The form of
232 the functional response curve may vary according to environmental conditions (Abrams 1982),
233 such as habitat heterogeneity (Hildrew and Townsend 1977; Kaiser 1983; Lipcius and Hines
234 1986), light intensity (Koski & Johnson 2002), host plant (Carter et al. 1984; Messina and Hanks
235 1998; De Clercq et al. 2000; Skirvin and Fenlon 2001), temperature (Thompson 1978; Gresens et
236 al. 1982; Bailey 1989; Mohaghegh et al. 2001; Mahdian et al. 2006; Li et al. 2007) and refuge for
237 prey (Lipcius and Hines 1986; Messina and Hanks 1998). In the current study, temperature
238 clearly influenced the magnitude of predator response to prey density (Fig.1). This may be
239 attributed to temperature-related changes in the metabolism and activity of predator and prey
240 (McCoull et al. 1998). Higher temperatures increased the functional response of *A. bipunctata*
241 by increasing attack rate and decreasing handling time. Similar observations were reported by
242 Thompson (1978), Gresens et al. (1982), Bailey (1989), Anderson et al. (2001) and Gotoh et al.
243 (2004). Our findings suggest that *A. bipunctata* spent more time in non-searching activities (e.g.

244 resting) at low temperatures (19°C), while more intensive searching and feeding occurred at
245 higher temperatures (above 23°C).

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

253 Functional responses may provide important information on the voracity of a biological
254 control agent, and on the effects of abiotic (e.g., temperature) or biotic (e.g., host plants) factors
255 on its foraging efficiency (e.g., Carter et al. 1984; Messina and Hanks 1998; De Clercq et al. 2000;
256 Mohaghegh et al. 2001; Skirvin and Fenlon 2001; Mahdian et al. 2006; Li et al. 2007). However,
257 functional response studies have been criticized because they are often performed in small
258 artificial arenas using unrealistic prey densities and do not consider spatial habitat complexities
259 or multispecies prey situations (van Lenteren and Bakker 1976; Murdoch 1983; O'Neil 1989,
260 1997; Kareiva 1990; Wiedenmann and O'Neil 1991; Messina and Hanks 1998; Hardman et al.
261 1999). Furthermore, functional responses do not consider crucial life history parameters of a
262 predator that may affect its value as a biological control agent. In the case of coccinellid
263 predators, the selection of prey patches by female adults is determined by expectations of
264 future bottlenecks in prey abundance (Dixon 2000). Many aphidophagous predators have
265 evolved the ability to attack prey colonies at an early stage of development to maximize the
266 fitness of their offspring. Dixon (2000) proposed that the most important attribute of an

267 effective biological control agent is the rate of its development relative to that of its prey, i.e.
268 the generation time ratio. According to this hypothesis, if the developmental rate of a predator
269 is similar to or faster than that of the prey then the predator is potentially capable of
270 suppressing the prey population. This concept would render *A. bipunctata* and other
271 aphidophagous coccinellids ineffective biological control agents, given the high intrinsic rates of
272 increase of most aphid species (Dixon 2000). However, advanced larval stages are released in
273 relatively high numbers in many augmentative biological control programmes using
274 aphidophagous coccinellids (e.g., Ferran et al. 1998; Wyss et al. 1999a,b). Commercial
275 packagings of *A. bipunctata* usually contain second to third instars (J. Vermeulen, BioBest NV,
276 personal communication). In such an inundative approach the objective is short term pest
277 suppression by the released larvae and the resulting adults rather than long term control of the
278 aphid populations. In addition, *A. bipunctata* larvae can be released in aphid hot spots rather
279 than in the whole crop.

280 The current study shows that *A. bipunctata* displays relatively high predation rates on
281 *M. persicae* at a wide range of temperatures, indicating its potential for augmentative releases
282 against the green peach aphid. Functional response models have served as a basis for
283 developing ecological theory on foraging behaviour and tritrophic interactions between plants,
284 prey and predators (or parasitoids) (Holling 1959; Hassell 1978; Messina and Hanks 1998; Tully
285 et al. 2005). Measures of voracity from functional response experiments may be indicative of
286 the value of coccinellid predators as augmentative biological control agents and provide a basis
287 for determining release rates appropriate for various aphid densities. However, robust
288 experimental assessment of functional responses remains difficult and certain behavioural
289 responses that are crucial in a biological control context cannot be taken into account in the
290 experimental design (van Lenteren and Bakker 1976, 1978; Tully et al. 2005). For instance,

291 laboratory studies may indicate the predation potential of *A. bipunctata* when aphids are
292 abundant, but they do not consider cannibalism or emigration of the predator that may occur
293 when aphid populations start to decline, leaving few predators in the crop in case the aphids
294 would resurge. Therefore, more field studies are needed to understand the foraging behaviour
295 of *A. bipunctata* in different cropping systems, in order to design practical release strategies for
296 this coccinellid.

297

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299

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471

472 **Table 1** Results of logistic regression analysis of the proportion of *M. persicae* nymphs (3rd and
 473 4th instars) eaten by adult females of *A. bipunctata* on initial prey density at different
 474 temperatures

475

Temperature (°C)	Coefficient	Estimate	SE	Chi Square	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_{C3})	-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_{C3})	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_{C3})	6.568E-6	7.798E-6	0.7096	0.3996

476

477

478 **Table 2** Parameters estimated by the random predator equation and corresponding asymptotic
 479 95% confidence intervals (CI) indicating functional response of adult females of *A. bipunctata* to
 480 densities of *M. persicae* 3rd-4th instars at different temperatures

481

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

482

483 *a: attack rate (on a 20-25 cm² leaf area); T_h: handling time

484

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

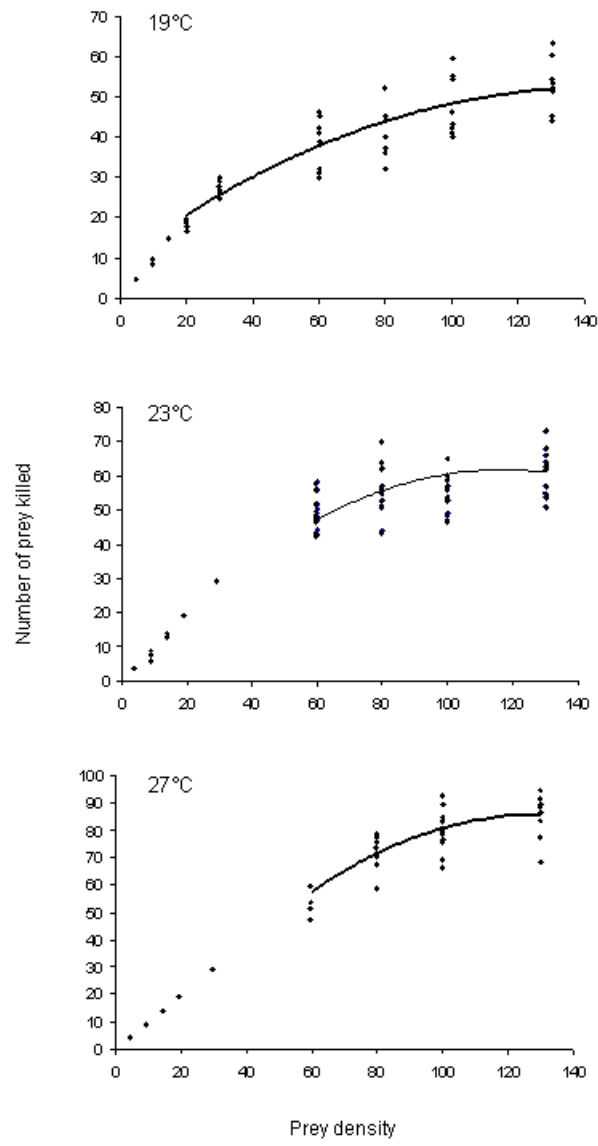


Fig. 1.