

# Functional response of a generalist insect predator to one of its prey species in the field

DOMINIQUE SCHENK and SVEN BACHER

Zoologisches Institut, Universität Bern, Baltzerstr. 6, CH-3012 Bern, Switzerland

## Summary

1. The shield beetle *Cassida rubiginosa* Müller (Coleoptera, Chrysomelidae) is one of the most prominent herbivores on creeping thistle, *Cirsium arvense* (L.) Scop. and is considered as a biological control agent against this weed. In order to investigate if augmented densities of this species could be sustained, predation on *C. rubiginosa* larvae was studied in the field with the aid of continuous video surveillance of individual prey during three seasons at two different study sites.
2. The paper wasp *Polistes dominulus* Christ (Hymenoptera, Vespidae) was responsible for 99.4% predation on *C. rubiginosa* larvae at both study sites. Prey densities were always reduced to a few individuals at the sites after a few days only. Thus, *P. dominulus* may annihilate the effect of augmentative releases of the beetle as a biocontrol agent.
3. *P. dominulus* showed no aggregation in patches of high host density (numerical response). The observed density dependence was attributed to the functional response of the wasp.
4. *P. dominulus* showed a Type III functional response. In mark-and-recapture experiments we found no indication that this type of functional response was the result of single wasps specializing on this particular prey type.
5. Type III functional responses in generalists can result by switching to prey species which become temporarily abundant. Since in a natural setting a mixture of prey species coexists in different abundance and which are differentially accepted by generalist predators, it is imperative to study their functional response in the field.

*Key-words:* field study, *Polistes dominulus*, population regulation, predator complex, remote video surveillance.

*Journal of Animal Ecology* (2002) **71**, 524–531

## Introduction

The functional response of a predator is a key factor in the population dynamics of predator–prey systems. The functional response can determine if a predator is able to regulate the density of its prey (Murdoch & Oaten 1975). For this to be the case the functional response must show density dependence, i.e. the predator must respond to higher prey densities by consuming an increasing proportion of the available prey over a range of prey densities. Such functional response curves are classified as Type III (Holling 1966), and are characterized by their sigmoid shape when plotting the number of prey items eaten by the predator against the number of prey available.

A Type III response can be generated in nature, for example by prey switching on the part of the predator.

Discussions of switching focus on the density of one prey type relative to the densities of alternatives, whereas functional responses are based only on the density of the single prey type being considered. Nevertheless, in nature, absolute and relative densities are likely to be correlated, and switching is therefore likely to lead to a Type III functional response (Begon, Harper & Townsend 1996). The functional response of a generalist predator to a single prey species determined in the laboratory may be of little value for predicting predator behaviour to a variety of prey types and densities, as found under natural conditions. It is therefore imperative to determine functional responses of not strictly monophagous predators in the field. Because of the secretive nature of predation events most field studies on functional responses so far involved large vertebrate predators like foxes (Angerbjorn 1989; Pech *et al.* 1992; White, White-Vanderbilt & Ralls 1996; Reid, Krebs & Kenney 1997; O'Mahony *et al.* 1999; Elmhagen *et al.* 2000), wolves (Dale, Adams & Bowyer 1994; Messier 1994; Messier 1995; Bergerud & Elliott 1998; Hayes & Harestad

Correspondence: Dominique Schenk, Zoologisches Institut, Baltzerstr. 6, CH-3012 Bern, Switzerland. Tel: + 41 31 6314525. Fax: + 41 31 6314888. E-mail: dominique.schenk@zos.unibe.ch

2000), coyotes (Windberg & Mitchell 1990; Patterson, Benjamin & Messier 1998; O'Donoghue *et al.* 1998) or birds (Caldow & Furness 2001; Wanink & Zwarts 1985), whose association with particular prey species are fairly well known.

In contrast, field studies on the functional response of smaller predators, in particular insects, in the field are almost absent. The only true field study on the functional response of insect predators is, to our knowledge, the one by Van den Berg *et al.* (1997), who calculated predation rates by direct field observations of individual coccinellid and staphylinid predators at various densities of aphids. However, direct observations are very time-consuming in order to obtain a reasonable number of predation events, and are probably not feasible for mobile predators preying on non-gregarious prey. Data from the study by Van den Berg *et al.* (1997), for example, did not allow for a rigorous testing of the type of the functional response due to the low number of data points.

Recently, remote video surveillance has been suggested as the method of choice for non-intrusive observation of predator-prey interactions in the field because many prey individuals can be observed simultaneously (Kidd & Jarvis 1996). Video techniques have been used extensively in laboratory studies but so far were rarely applied to study insects in the field (Wratten 1994; Meyhöfer 2001). We used remote video surveillance to study the predator complex of larvae of the shield beetle *Cassida rubiginosa* Müller (Coleoptera, Chrysomelidae). This species is considered as a potential native biological control agent against creeping thistle, *Cirsium arvense* (L.) Scop, one of the world's worst weeds in agriculture (Holm *et al.* 1977). In order to investigate if augmented densities of *C. rubiginosa* could be sustained, we also quantified density dependent predation by manipulating prey densities in the field.

## Methods

### EXPERIMENTAL SITE AND SET-UP

Fourth and early fifth instar larvae of *C. rubiginosa* used in the experiments were reared in the laboratory on cut shoots of creeping thistle. In 1999 and 2000, the experiments were conducted on a natural 30 m<sup>2</sup> patch of *c.* 800 *C. arvense* shoots in Bern (site 1). This patch was part of a larger, partly uncultivated meadow of about 1000 m<sup>2</sup> with a mixture of flowering plants, and was surrounded by orchard trees and hedges. In 2001, the experiment was carried out on an ecological compensation area of 6 × 150 m located within arable farmland in Belp, near Bern, dominated by creeping thistle, teasel (*Dipsacus fullonum* L.), parsnip (*Pastinaca sativa* L.), burdock (*Arctium lappa* L.) and grasses (site 2). The thistle patch was 50 m<sup>2</sup> in size and included approximately 300 *C. arvense* shoots. Thistles were searched for naturally occurring *C. rubiginosa* larvae which were removed prior to the experiments. Predation on *C. rubiginosa* was investigated by continuous

video surveillance of individual beetle larvae. This was feasible because *C. rubiginosa* larvae behave rather sedentary, generally remaining on the same leaf throughout the day. In previous experiments we established that *C. rubiginosa* larvae will not disperse to plants other than thistles, and that mortality from causes other than predation is virtually nonexistent in late *C. rubiginosa* larval instars (S. Bacher, unpublished). Thus, all larvae missing could be attributed to predation.

Predation registration took place from 2–8 August 1999, from 26 May to 16 August 2000 and from 4 June to 7 August 2001. Four video cameras were installed in autumn 1999, nine cameras in 2000 and 2001.

### VIDEO EQUIPMENT AND RECORDING

Video recording equipment in the field consisted of one infrared (for day and night observations) and eight colour cameras (CCD colour camera module, Conrad Electronics), and two sets of each one time-lapse video cassette recorder (VCR, Panasonic AG-6124) and one multiplexer (Sony YS-SX310P). The use of a multiplexer allows that the feed of multiple cameras can be recorded on a single VCR. Both sets were placed in a weatherproof metal box (57 × 37 × 33 cm) in the field adjacent to the thistle patches. The boxes were ventilated by a fan (10 cm diameter) to avoid overheating of the equipment inside the box. The power for the equipment (220 V) was supplied from the nearest building. The sets were equipped with four and five cameras, respectively. Cameras were fixed to poles and adjusted with the aid of a portable video monitor (b/w LCD monitor, Conrad electronics) such that they focused on a single *C. arvense* leaf with a larva feeding on it. Video recordings were done in 24-h time-lapse mode. Thus, a conventional E-180-min video tape recorded the events of four and five cameras, respectively, for 24 h. The VCR setting allowed for a resolution of one picture every 1.28 s from each camera. Cameras were checked several times each day and re-focused on the larvae if necessary. Missing larvae were replaced. Tapes were searched for predation events in the laboratory on a third VCR-multiplexer set connected to a video monitor (Sony PVM-14 N6E). Recordings from cameras were investigated only if the larva disappeared during the observation period. Predation events were copied to VHS video tape on a conventional VCR (Panasonic NV-FJ610) for analysing and archiving purposes.

### DENSITY-DEPENDENT PREDATOR RESPONSE

In 2000 and 2001, prey densities were manipulated during 42 and 30 consecutive days, respectively, starting in the beginning of June with prey densities of 58 and 69 individuals, respectively. Larvae were distributed uniformly over the patch. Each early morning the entire thistle patch was searched for all remaining larvae in order to determine predation rates of the previous day. In addition, once or twice per week the

density (number of foraging predators at the site) of the predator species identified by video analysis was determined during two hours in the early afternoon (peak activity); all predators observed foraging at the site were caught by sweep netting and released after the observation period. In 2000, all wasps captured were marked individually with numbered colour plates used for bee queens.

#### STATISTICAL ANALYSIS

We first analysed if density dependent predation rates were due to a numerical response of predators (i.e. aggregation in patches of high prey density) by linear regression of predator on prey density. Linear regression was also used to investigate the relation between predator density and weather data (air temperature, wind speed, relative humidity, percentage cloud cover; all data taken from 13:00 h) obtained from the Swiss meteorological station in Bern, Liebefeld. If independence of predator and prey density was found density-dependent predation rates were attributed to the functional response of predators. Because our experiments were conducted with prey depletion we used the 'random predator equation' (Rogers 1972) as a description of the functional response:

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

where  $N_e$  is the number of prey eaten by the predator,  $N_0$  the initial prey density,  $a$  the attack rate,  $T$  the time that predator and prey are exposed to each other, and  $T_h$  the handling time associated with each prey eaten. Equation 1 models a Type II functional response with a constant attack rate  $a$ . When the attack rate itself becomes a function of prey density, functional responses of Type III can be modelled (Hassell, Lawton & Beddington 1977). We used the most general useful form in which  $a$  is a hyperbolic function of  $N$  (Juliano 2001):

$$a = (d + bN_0)/(1 + cN_0) \quad \text{eqn 2}$$

For Type III responses, the precise form of the model incorporating prey depletion we used was thus:

$$N_e = N_0(1 - \exp((d + bN_0)(T_h N_e - T)/(1 + cN_0))) \quad \text{eqn 3}$$

Functional responses of Type II and III are difficult to discriminate; several studies focused on this problem (e.g. Trexler, McCulloch & Travis 1988; Casas & Hulliger 1994). To distinguish between Type II and Type III responses we first investigated if the attack rate  $a$  increased with prey density. The handling time  $T_h$  (defined as the time needed for a wasp to kill and eat a larva until take-off from the leaf) was determined from the video recordings. For each recording of a predation event the attack rate was calculated by solving eqn 1 for  $a$  (Hassell *et al.* 1977). We set the value of  $T$  to 24 h

in our experiment. Density dependence was analysed by Spearman's rank correlation. If a significant correlation was found, eqn 2 was fitted to the data using the non-linear least-squares curve-fitting procedure of Systat version 9. We also used a more sophisticated procedure to distinguish between Type II and Type III responses (Juliano 2001). We performed logistic regression of the proportion of larvae eaten as a function of initial prey density (Trexler *et al.* 1988). We first fitted a polynomial function

$$\frac{N_e}{N_0} = \frac{\exp(L_0 + L_1 N_0 + L_2 N_0^2 + L_3 N_0^3)}{1 + \exp(L_0 + L_1 N_0 + L_2 N_0^2 + L_3 N_0^3)}, \quad \text{eqn 4}$$

(Juliano 2001) where  $N_e/N_0$  is the probability a larva is eaten by a predator with the CATMOD procedure of SAS version 8.1. A criterion for separating Type II and Type III functional responses is to test for significant positive or negative linear coefficients in the expression fit by the method of maximum likelihood to data on proportion eaten vs.  $N_0$  (Juliano 2001). We applied non-linear least-squares regression of eqn 3 to our data for parameter estimation using the procedure NLIN in SAS. Non-significant parameters were removed from the model and the model recalculated until all parameters were significant. Although considered a less desirable choice for distinguishing between functional response types (Trexler *et al.* 1988),  $b > 0$  obtained by non-linear least-squares regression of equation 3 is sufficient to conclude that the functional response is of a Type III form (Juliano 2001).

## Results

#### PREDATOR SPECIES, PREY DENSITY AND PREY MORTALITY

Of the 157 video recordings of predation events during the three seasons, 156 (99.4%) showed the paper wasp *Polistes dominulus* Christ (Hymenoptera: Vespidae) as predator of *C. rubiginosa* larvae (site 1:  $N = 50$ ; site 2:  $N = 107$ , including one recording of a larva of *Chrysoperla carnea* Stephen preying on a *C. rubiginosa* larva). Predation events took place between 10:39 h and 17:27 h in 1999 and 2000 and between 10:12 h and 19:36 h in 2001, with activity peaks between 11:00 h and 17:00 h (site 1: 92%; site 2: 87.8%; Fig. 1). No predation was observed during the night.

The time-course of *C. rubiginosa* larval densities is shown in Fig. 2. In 2000, prey density dropped to three or two individuals on the site (after 16 days), remained constant at this level for 4 days, was increased to 30 larvae (after 20 days) and again decreased to a low level and stayed there for some days. The lowest density was one larva on the whole site. In 2001, prey density was increased six times over the experimental period. Between the peaks, prey density dropped to low density levels, with a minimum of one larva on the whole site. Daily number of *C. rubiginosa* larvae eaten by

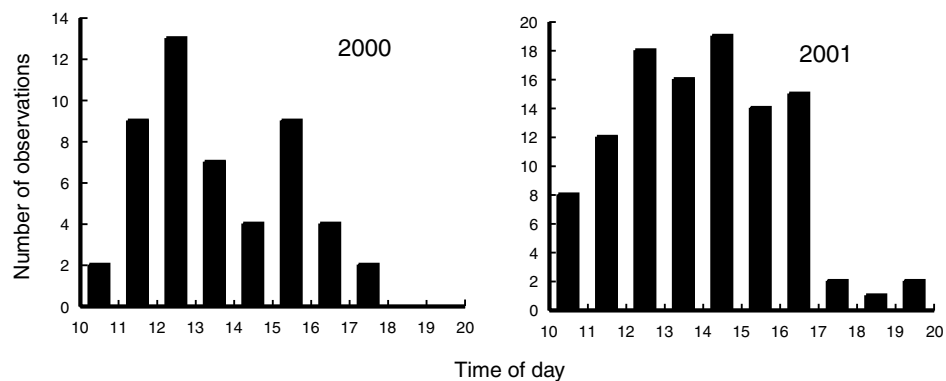


Fig. 1. Number of observations of wasps preying on *C. rubiginosa* larvae at different day times in 2000 and 2001, as recorded by video surveillance.

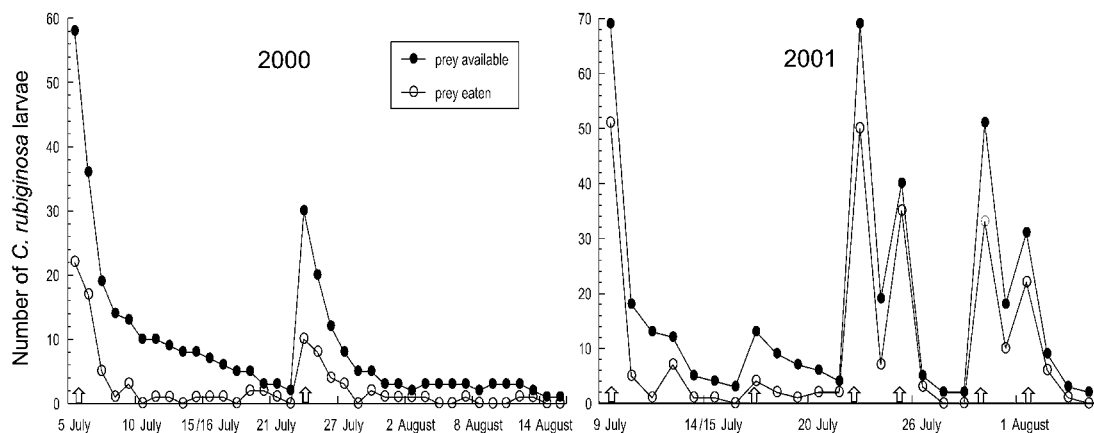


Fig. 2. Number of *C. rubiginosa* larvae at the study sites over the duration of the experiments in 2000 and 2001. Dark circles show prey available, open circles prey eaten. Arrows indicate the dates the prey densities were experimentally augmented.

predators ranged between 0 and 22 individuals in 2000 and between 0 and 51 in 2001 (Fig. 2).

#### PREDATOR DENSITY

Sweep-netting revealed a density of foraging *P. dominulus* at the study site of one to 12 wasps in 2000 and one to four wasps in 2001 during the 2-h sampling period. Predator density was independent of prey density (Table 1). Therefore, we assume a constant number of predators foraging at all prey densities during the experiment. Predator density did not vary with daily weather conditions (Table 1). Only one of the marked wasps was recaptured in 2000.

#### DENSITY DEPENDENCE OF HANDLING TIME AND ATTACK RATE

Because *P. dominulus* appeared in the video recordings virtually as the only predator, we attributed the observed density dependent predation to this species only. Since there was no numerical response of the predator during the experiment, the shape of the prey mortality curve is determined by the predator's functional response alone.

Table 1. Linear regressions of predator density on prey density and weather conditions ( $N = 6$ )

Factor	Year	Constant	Slope	<i>P</i>
Prey density	2000	5.57	-0.33	0.477
	2001	1.87	-0.021	0.476
Temperature (°C)	2000	-3.5	0.32	0.611
	2001	-1.74	0.18	0.357
Wind force (knots)	2000	4.95	-0.22	0.694
	2001	3.69	-0.25	0.375
Humidity (%)	2000	20.27	-0.34	0.251
	2001	7.84	-0.09	0.222
Cloud cover (octas)	2000	4.77	-0.34	0.632
	2001	3.76	-0.31	0.135

Handling time  $T_h$ , defined as the time period between landing of a wasp on a leaf with a *C. rubiginosa* larva and its take-off after the meal, was calculated from all suitable video recordings of predation during the experiment (2000:  $N = 30$ ; 2001:  $N = 77$ ). Handling times of *P. dominulus* lasted between 11 and 871 s in 2000 and 15 and 695 s in 2001, with a median of 54 (2000) and 73 s (2001; Fig. 3). Handling time  $T_h$  seemed to decrease with increasing prey density in both years, but this relation was only significant in the second year because of

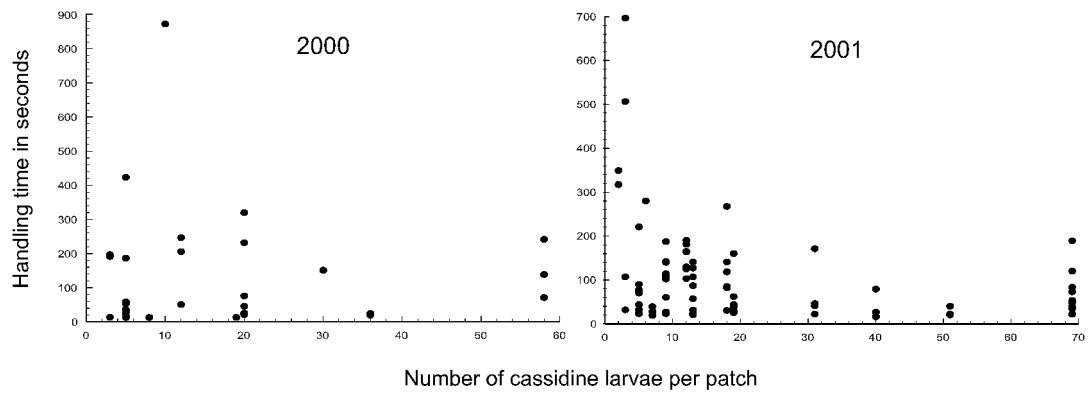


Fig. 3. Handling times of *P. dominulus* feeding on *C. rubiginosa* larvae at different prey densities in 2000 and 2001.

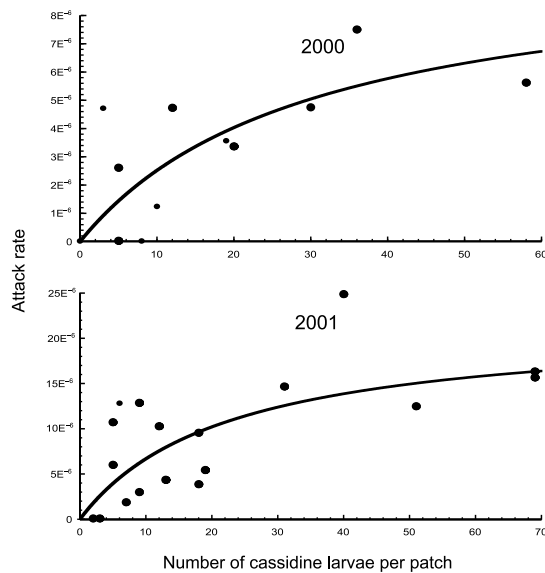


Fig. 4. Attack rates of *P. dominulus* at different prey densities in 2000 and 2001. Bold points indicate multiple (2–8) data points.

the larger number of recorded predation events in 2001 (2000:  $T_h = 138.48 - 0.34 N$ ,  $P = 0.864$ ,  $r^2 = 0.001$ ; 2001:  $T_h = 136.12 - 1.46 N$ ,  $P = 0.011$ ,  $r^2 = 0.084$ ). However, because the proportion of the variance explained by the regression was small in both years we used the median of the handling time to calculate attack rates. Calculated attack rates  $a$  (from the 30 and 77 video recordings, respectively) yielded values between zero and  $7.5E^{-6}$  (2000) and zero and  $2.4E^{-5}$  (2001). Attack rates increased with increasing prey densities (Spearman's

rank correlation 2000:  $r_s = 0.789$ ,  $P < 0.001$ ; 2001:  $r_s = 0.604$ ,  $P < 0.001$ ; Fig. 4). Curve-fitting yielded  $a = 1.3E^{-7} + 3E^{-7}N/1 + 0.03 N$  ( $r^2 = 0.6$ ) in 2000 and  $a = 2.6E^{-6} + 5.5E^{-7}N/1 + 0.021 N$  ( $r^2 = 0.48$ ) in 2001 (Fig. 4), indicating Type III functional responses for the data of both years.

#### DETERMINING THE FUNCTIONAL RESPONSE

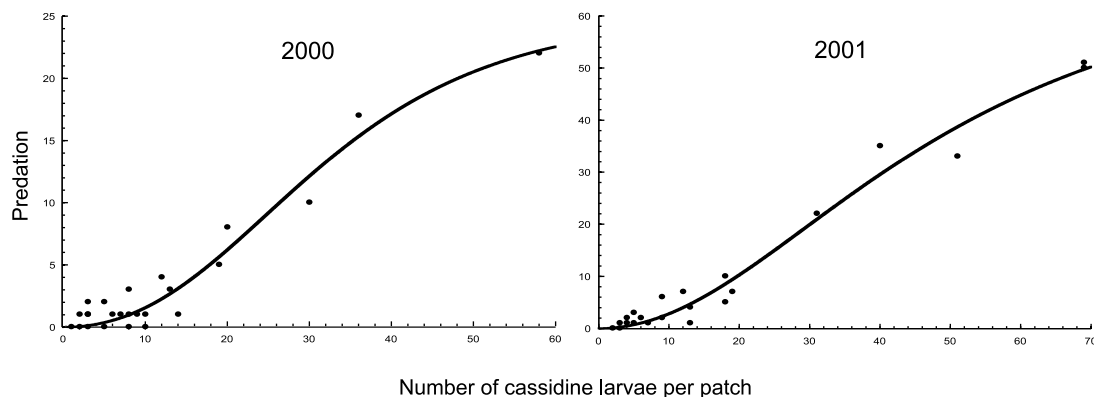
In both years, none of the parameters except the intercept  $L_0$  estimated by logistic regression were significant (Table 2). The linear parameter  $L_1$  of the data from 2000 is negative indicating a Type II functional response, whereas  $L_1$  of the 2001 data is positive and the quadratic parameter  $L_2$  negative, indicating a Type III curve. A lack of finding significant support for a Type III functional response with the method of logistic regression is not sufficient to conclude that the underlying data was not generated by a Type III functional response. Parameter estimates for eqn 3, as performed by NLIN in SAS, revealed that in both years  $b$  and  $T_h$  were significant and positive, while  $c$  and  $d$  were not significant, and therefore removed from the model (Table 3). This indicates that  $a$  was linearly related to  $N_0$  (eqn 2, and the functional response of Type III in both years. The choice of  $T$ , the total time predator and prey were exposed to each other, did not affect the proportion of variance explained by the regression (2000:  $r^2 = 0.96$ ; 2001:  $r^2 = 0.98$ ), but the size of the estimates for  $b$  and  $T_h$ . To achieve realistic and meaningful parameter estimates we set the actual daily time of exposure of predators and prey in accordance with the activity period of wasps (Fig. 1) to 6 h

Table 2. Maximum likelihood estimates of the logistic regression of proportion eaten on prey density (eqn 4)

Parameter	Estimate		SE		P	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
$L_0$	-1.20	-1.59	0.49	0.54	0.015	0.003
$L_1$	-0.073	0.095	0.083	0.065	0.38	0.14
$L_2$	0.0051	-0.0007	0.0034	0.0020	0.13	0.72
$L_3$	$-6.0E^{-5}$	$-1.65E^{-6}$	$3.7E^{-5}$	$1.8E^{-5}$	0.09	0.93

**Table 3.** Least squares estimates of the reduced model (eqn 3,  $d = c = 0$ ;  $T = 6$  h)

Source	d.f.		Sum of squares		Mean square	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
Regression	2	2	976.9	8058.4	488.4	4029.2
Residual	35	22	45.1	141.6	1.3	6.4
Uncorrected total	37	24	1022.0	8200.0		
(Corrected total)	36	23	793.2	5719.3		
Parameter	Estimate		Asymptotic SE			
	Site 1	Site 2	Site 1	Site 2		
$b$	0.0039	0.0074	0.0005	0.0011		
$T_h$	0.169	0.068	0.021	0.011		

**Fig. 5.** Functional response Type III (sigmoid) of *P. dominulus* in 2000 and 2001.

rather than the total duration of each experiment (24 h). Handling time estimated by the model was  $0.17 \pm 0.02$  h (= 10.2 min) at site 1 in 2000 and  $0.07 \pm 0.01$  h (= 4.2 min) at site 2 in 2001 (Table 3). The fit of the final model is shown in Fig. 5.

## Discussion

Video observations showed an unexpected predator spectrum. With one exception, we registered exclusively the paper wasp *P. dominulus* as predator of *C. rubiginosa* larvae during three seasons and at two different sites. One reason may be that *C. rubiginosa*, as do other shield beetle larvae, carries a faecal shield over its abdomen which provides mechanical protection against predation (Eisner, van Tassell & Carrel 1967). However, this protection is not perfect. For example, Eisner & Eisner (2000) showed that while the faecal shield of *Haemyspherota cynaea* (Say) larvae (Cassidinae) was effective against most predators, a single carabid species (*Calleida viridipennis* Say) was able to circumvent the protection (due mainly to its large body size), feeding on *H. cynaea* larvae in the field. This seems to be similar in our system. While small generalist predators such as ants, predatory bugs and lacewing larvae were abundant on both sites (personal observation) only the large *P. dominulus* actually utilized *C. rubiginosa* larvae as prey.

Until now, Vespidae have never been reported as important predators of shield beetles. Only Olmstead (1991) reported vespid wasps preying on shield-bearing larvae of *Deloyala guttata* Olivier. A literature survey by Cox (1996) lists Nabidae, Pentatomidae, Asilidae, Coccinellidae and Formicidae as field predators of Cassidinae. All these records, however, are based on anecdotal observations only. On several occasions, we also observed lacewing larvae preying on *C. rubiginosa* larvae in the field at different sites (personal observation). Several authors studied the defence of shield beetles against generalist predators in the laboratory (e.g. Eisner *et al.* 1967; Olmstead & Denno 1993; Müller & Hilker 1999; Eisner & Aneshansley 2000; Eisner & Eisner 2000). However, in all these studies the authors failed to establish the importance of their predators in the field. Our study is the first detailed analysis of predator–cassidinae interactions in the field. We believe that it is crucial to assess predation in a field setting in order to correctly interpret the importance of a defence mechanism.

In a previous study we found that predation is a serious mortality factor in late *C. rubiginosa* instars, while the early instars suffer mainly from abiotic mortality factors (S. Bacher & L. Kaufmann, unpublished). Under field conditions, the *C. rubiginosa* instars used in this study require about 5–8 days to reach the pupal stage (Ward & Pienkowski 1978; D. Schenk &

S. Bacher, unpublished). After this time, larval densities were almost always reduced to only few individuals on the entire site (Fig. 2). Moreover, in the field *C. rubiginosa* pupates in the vegetation glued to leaves or stems of herbaceous plants. Therefore, pupae may also be prone to predation by wasps. Thus, the presence of *P. dominulus* may seriously reduce local densities of *C. rubiginosa*, and may even lead to the local extinction of beetle populations. In reducing beetle densities it also reduces the impact of *C. rubiginosa* larvae on its host plant creeping thistle (Bacher & Schwab 2000), and may annihilate the effect of augmentative releases of the beetle as biocontrol agent.

Handling times estimated by the model were longer than only the time needed to kill and eat a prey as revealed by the video analysis. Considering the travel time for the wasp from and to the colony and the time needed to pass the food to other colony members handling times of 10 min at site 1 and 4 min at site 2 as suggested by the model seem realistic. The difference between the handling times at both sites can most probably be attributed to the fact that at site 2 the wasp colonies were located adjacent to the experimental site, whereas at site 1 the location of the wasp colonies could not be discovered in the direct vicinity of the site and was probably farther away.

A likely mechanism how functional responses of Type III could be generated in generalists such as *P. dominulus* is that predators preferentially hunt for prey that become temporarily abundant. This kind of learning is common in generalist predators (e.g. Murdoch 1969) and will lead almost invariably to a Type III functional response. In the mark-and-recapture experiment we found no indication that the Type III functional response was the result of single wasps specializing on this particular prey type; we rather assume that a large fraction of the wasp population switched to the beetle as prey. Functional responses of Type II were often found in laboratory or field cage studies where only single prey species were offered. However, laboratory studies do not take into account alternative prey as it occurs in the field. Therefore, the prevalence of Type II functional responses found under restricted conditions may overestimate their occurrence and importance in nature. We recommend determination of functional responses of not strictly monophagous predators, most of which are attacking different prey species, in the field.

### Acknowledgements

We thank Britta Tschanz and Ursula Wunder for their field assistance, Thomas Friedli and Tanja Steiner for statistical advice and the two anonymous referees for commenting on a previous version of this manuscript. This study was funded partly by the Swiss National Science Foundation through the National Centre of Competence in Research (NCCR) 'Plant Survival'.

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Received 12 November 2001; accepted 4 February 2002