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Ratio-dependent predation in a field experiment with wasps

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Abstract. The functional response is a key component of trophic interactions since it quantifies the per capita rate of prey consumption. Determining whether this rate depends on the prey density only (which is the standard assumption), on both prey and predator densities, or simply on their ratio is essential to understand interacting populations. Several experiments have convincingly demonstrated ratio dependence but, with very few exceptions, they were conducted in laboratory conditions. The difficulty of collecting the required data (initial prey density, prey consumption, predator density) probably explains the lack of evidence from functional responses observed in natural systems. A field experiment was previously conducted with a paper wasp and its prey, shield beetle larvae. Both densities were manipulated and the prey consumption was measured. A first analysis led to the conclusion that the functional response of the wasps depended on both prey and predator densities but could not be considered being ratio dependent.

Here, we perform an improved analysis of these data, making better justified assumptions and using more appropriate statistical methods. We fit several functional response models to the data and select the best one with information-theoretic criteria. We also estimate the model parameters and their confidence intervals. This more reliable analysis significantly modifies the original conclusion. Both model selection and parameter estimation indicate that ratio dependence governs the functional response of paper wasps preying on shield beetles in the field. Therefore, ratio dependence is not a laboratory artefact and should be more systematically considered as a potential model for describing functional responses.

Key words: *Cassida rubiginosa*; field experiment; functional response; model selection; mutual interference; *Polistes dominulus*; predation; predator dependence; ratio dependence.

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INTRODUCTION

The functional response g (the instantaneous rate of prey consumption by an average predator) is a key factor to understand the functioning of natural predator-prey systems. The functional

response had originally been defined as a function of the prey density only [$g = g(N)$] but many studies have shown that the predator density also influences the individual predation rate [$g = g(N, P)$]. This is known as “predator dependence” (Arditi and Ginzburg 1989). From

an ecological point of view, the question of the way in which the functional response depends on the predator density is critical because this dependence plays a key role for population regulation, system stability, and community structuring (e.g., Arditi and Ginzburg 1989, Akçakaya et al. 1995, Hassell 2000, Rall et al. 2008). It has been proposed that the functional response is likely to depend approximately on both prey and predator densities simply via their ratio [$g(N, P) = g(N/P)$] (Getz 1984, Arditi and Ginzburg 1989). While the existence of predator dependence is now widely accepted (e.g., Begon et al. 2006, Gotelli 2008, Krebs 2009), a number of authors consider ratio dependence as unlikely to take place in natural systems or complain for a lack of mechanistic explanations. In their view, both prey density and predator density affect the functional response independently [$g = g(N, P)$]. Mathematically, this implies one more variable and a higher-dimensional parametric space. In contrast, ratio dependence is of the same dimensional complexity as the original prey-dependent view. Some aspects of this debate were discussed by Abrams and Ginzburg (2000) and the whole theory of ratio dependence is treated comprehensively in a recent book by Arditi and Ginzburg (2012), in which Chapter 5 reviews the controversy. Moreover, many mechanisms have been identified as leading to the emergence of ratio dependence (see Chapter 4 of Arditi and Ginzburg 2012).

The fact that the functional response is an instantaneous concept prevents any immediate observation of it. However, it can be calculated from the direct observation of the number of prey eaten over a finite period of time. Following Holling (1959), hundreds of experiments have measured the dependence of the functional response on the prey density N . Several dozens have measured the dependence on the predator density P , a dependence known as ‘interference’ (see, e.g., the reviews of Hassell 1978, 2000 and DeLong and Vasseur 2011). However, surprisingly few experimental studies have studied the bivariate dependence on (N, P) , which is clearly what is needed in order to confirm or refute prey dependence, predator dependence or ratio dependence. The few existing studies deal with various systems like microbial systems (Cabrera F, 2011), aquatic invertebrates in microcosms

(Hansson et al. 2001, Kratina et al. 2009), arthropod predators (Arditi and Akçakaya 1990, Reeve 1997, Schenk et al. 2005, Hauzy et al. 2010), insect parasitoids (Arditi and Akçakaya 1990, Mills and Lacañ 2004), big mammals (Owen-Smith 2002, Vucetich et al. 2002, Jost et al. 2005). Assessing the impact of prey and predator densities on the functional response is not a straightforward operation in natural systems. Therefore, most experiments have been conducted in artificial or semi-natural settings. This is really problematic because a classic explanation of ratio dependence rests on spatial heterogeneity and spatial behaviours of prey and predators (Arditi and Saiah 1992, Akçakaya et al. 1995, Poggiale et al. 1998, Cosner et al. 1999, Arditi et al. 2001, Tyutyunov et al. 2008). These features are difficult to reproduce in non-natural settings. Evidence from natural systems generally rests on indirect observations used to infer the functional response, for example from positive correlations between the abundances of consecutive trophic levels (Ginzburg and Akçakaya 1992) or from time series (Jost and Arditi 2000, 2001).

In this article, we re-analyze a unique experiment in which direct measurements of the functional response were performed in a natural setting by Schenk et al. (2005). They manipulated in the field the densities of a predator, the paper wasp *Polistes dominulus*, and its prey, shield beetle larvae (*Cassida rubiginosa*), and monitored the prey individually with video equipment. The analysis of their observed data led these authors to conclude that the predator functional response was neither purely prey dependent nor purely ratio dependent but intermediate (Schenk et al. 2005). We later realized that the methods used for organizing the data, for parameter estimation, and for model selection could all be improved in significant ways, and we suspected that more reliable results obtained from the same observations could lead to different conclusions.

A first improvement relates to the predator densities used for the analyses. Schenk et al. (2005) assumed a constant daily number for the abundance of active predators, which was calculated as the sum of the numbers of predators present during each of the activity hours. Three ways for refining the determination of predator densities are explored in the present study. In contrast with Schenk et al. (2005) who

determined the hourly numbers of predators in different ways in the different activity hours, we use a homogeneous approach that will be explained later. Then, we use the number of predators being present instead of the cumulated one as in Schenk et al. (2005), to be consistent with the definition of the functional response as a function of the “instantaneous” numbers of prey and predators present at a given time. Finally, we take account of the variations in the numbers of active predators in the course of the day rather than using a constant daily average, in order to make full use of the rich information that had been collected.

For computational reasons, Schenk et al. (2005) did not estimate all functional response parameters from the same data set: while the interference coefficient m was estimated with the 2005 data, the handling time and the searching efficiency were estimated from the previous experiment of Schenk and Bacher (2002) conducted at the same location. (This previous experiment observed the response to prey density only; the predator density was not varied.) However, the environmental conditions that prevailed during the 2002 experiments were quite different and it is very likely that the parameter values (particularly the searching efficiency) were not the same. In the present article, we estimate all parameters simultaneously from the same data set, avoiding this potential bias. This is the second improvement of the present paper.

A third major improvement is in the model selection procedure. Instead of relying entirely on the estimation of the mutual interference coefficient m , we fit a family of different functional response models, including the one used by Schenk et al. (2005). We then use information-theoretic criteria to compare the different models and select the best one (Burnham and Anderson 1998).

As will be seen, this improved analysis lead to the very clear conclusion that this predator-prey system follows a ratio-dependent functional response, rather than the previous conclusion of an “intermediate” degree of predator interference that was reached in 2005. In the context of the debate over the validity of the ratio-dependent hypothesis, we consider it necessary to publish the revised conclusion obtained from the same

data with improved analytical methods.

MATERIAL AND METHODS

Experimental data

Full details of the experimental setup are available in Schenk and Bacher (2002) and Schenk et al. (2005). Schenk and Bacher (2002) measured the predation rates of wasps on prey larvae presented at various densities. These prey densities N were set by removing all larvae occurring naturally in the experimental patch and distributing uniformly a given number of larvae reared in the lab. The naturally occurring predator density, i.e., the number of wasps observed foraging at the experimental site during one hour of the peak wasp activity, was approximately constant, uncorrelated to the prey density. Thus, this was a standard measurement of the response to prey density alone. This first experiment led the authors to the conclusion that the predator *P. dominulus* had a type-III functional response. Fitting the following classic type-III model,

$$g(N) = \frac{bN^2}{1 + bhN^2} \quad (1)$$

they estimated its two parameters b (the proportionality factor between predator density and searching efficiency) and h (the handling time).

Although the predator abundance was treated as a constant number across various prey densities, the authors monitored the variations of wasp activity during the day from the video recordings of predation events. We use the latter data and similar observations obtained in later years (Tschanz et al. 2007) to fit a gamma distribution in order to establish a predator activity profile during the day (Fig. 1). The consequences of these activity variations are studied in the present paper (see below).

Using basically the same experimental setup, Schenk et al. (2005) tested the influence of predator density in addition to the influence of prey density. For this, they conducted more complex experiments in which they manipulated not only the prey density, but also that of the predators by opening cages containing wasp nests in the immediate vicinity of the prey. They combined eight prey densities ($N = 2, 4, 6, 8, 10, 20, 30, 40$) with four numbers of predator cages (c

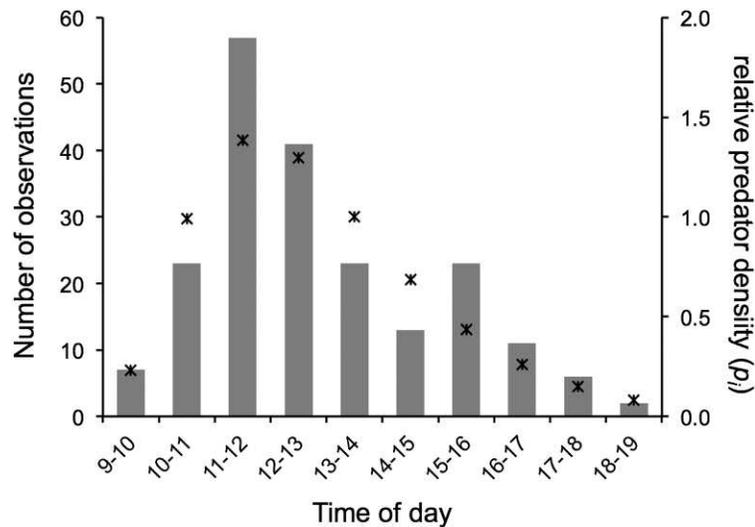


Fig. 1. Activity profile of predators during a day. This profile is obtained by fitting a gamma distribution (stars) to data (bars). The data correspond to the cumulated numbers of wasps preying on *C. rubiginosa* larvae at different day times in 2000, 2002, 2004, as recorded by video monitoring. The p_i values correspond to the relative activity in comparison with the 13–14 h value, which is set to 1. The hourly predator numbers during the day (P_i) are obtained by multiplying the p_i by M_c , the mean number of wasps caught during the 13–14 h slot ($M_0 = 1.75$, $M_{1,2,3} = 3.708$).

= 0, 1, 2, 3) in a factorial design. Each of the 32 experimental bivariate combinations was conducted on a different day. The numbers of prey being consumed were measured from the counts of the prey remaining at the end of the day (Fig. 2).

The authors assessed the numbers of active predators foraging at the experimental site by sweep netting during one hour (13 h–14 h). By combining these observations with the gamma distribution describing the daily predator activity profile, effective hourly estimates of wasp numbers (P_i) can be reconstructed (Fig. 1). These hourly predator numbers differ from those used by Schenk et al. (2005) for three reasons. First, the activity profile in the current study calls on a gamma distribution fitted to data that include several years of observation (instead of a single year) and is extended upon ten time intervals (instead of eight). Second, according to the observations of Schenk et al. (2005) the number of predators caught during the 13 h–14 h hour (M_c) is not significantly different with $c = 1, 2$, or 3 open cages ($M_1 = 4.375$, $M_2 = 3.625$, $M_3 = 3.125$; Kruskal-Wallis test, $p = 0.89$). Therefore, these three cases are merged in the present study ($M_{1,2,3} = 3.708$, $n = 24$). Comparing with the

natural density (no cage open; $M_0 = 1.75$, $n = 8$), there is a significant difference between these two values (Mann-Whitney U -test, $p = 0.031$). Thus, only two predator densities can be distinguished (and not four). Third, unlike Schenk et al. (2005) who used the actual number of foraging wasps for the 13 h–14 h time interval but the average number M_c for all other intervals, we reconstruct all hourly abundances from the activity profile and from M_0 and $M_{1,2,3}$, as explained in the legend to Fig. 1.

Functional response models

Combining the standard type-II prey-dependent model of Holling (1959) with the interference model of Hassell and Varley (1969), Arditi and Akçakaya (1990) proposed the following expression for a type-II predator-dependent model of the functional response:

$$g(N, P) = \frac{\alpha N / P^m}{1 + \alpha h N / P^m} \quad (2)$$

where N and P are the prey and predator densities respectively, α is a measure of the searching efficiency, h the handling time, and m the mutual interference coefficient. According to

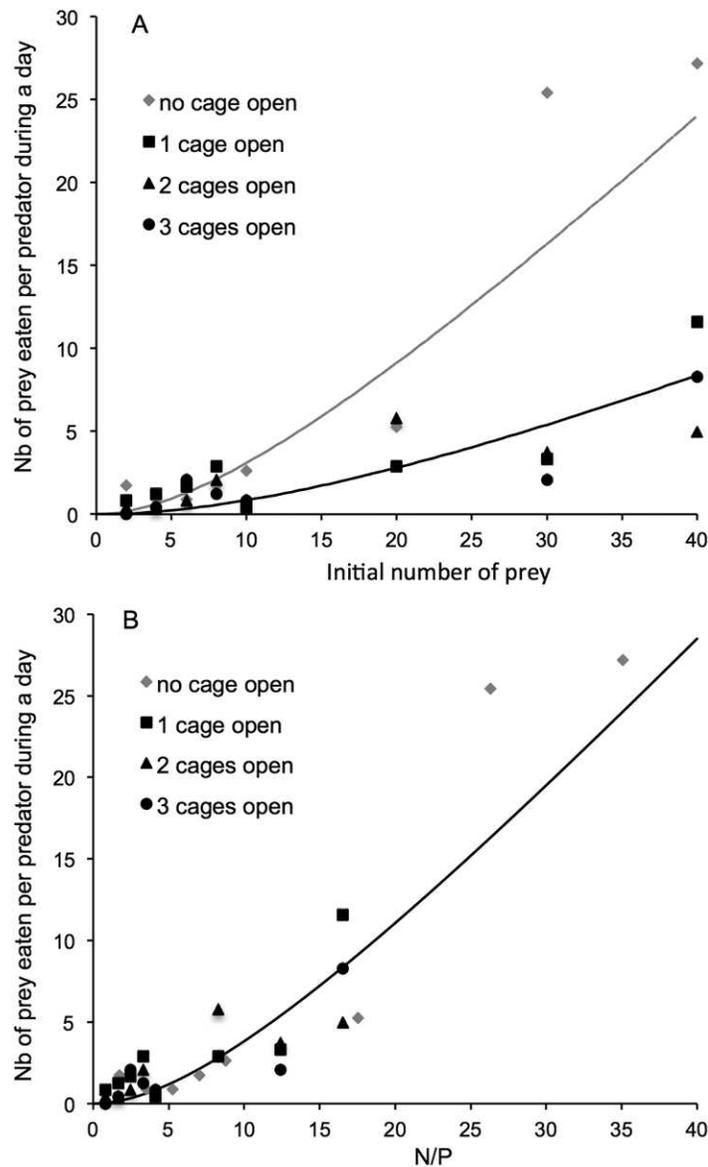


Fig. 2. Numbers of prey eaten per predator during a day when 0, 1, 2, or 3 cages were open as a function of (A) the initial density of prey and (B) the ratio between the initial number of prey and the average number of predators. Curves correspond to the best-fitting model (model 4, see Table 4). In (A), the curves at low predator density (grey line, no cage open) and at high predator density (black line, 1, 2, or 3 cages open) are distinct. In (B) the same curve stands for all predator densities.

the classification proposed by Holling (1959), Eq. 2 simplifies to a type-I functional response if $h = 0$. This functional response is purely prey dependent for $m = 0$, purely ratio dependent for $m = 1$ and predator dependent for the other values of m .

A type-III (i.e., sigmoid) functional response Hence:

can be obtained by replacing the searching efficiency α by a function that increases linearly with N/P^m :

$$\alpha \rightarrow \left(\alpha + \beta \frac{N}{P^m} \right). \quad (3)$$

$$g(N, P) = \frac{(\alpha + \beta \frac{N}{P^m}) \frac{N}{P^m}}{1 + (\alpha + \beta \frac{N}{P^m}) h \frac{N}{P^m}}. \quad (4)$$

The original type-II Arditi-Akçakaya model (Eq. 2) is retrieved with $\beta = 0$. The type-III predator-dependent functional response used by Schenk et al. (2005) corresponds to the special case of Eq. 4 with $\alpha = 0$, but there is no a priori reason to make this restriction.

Handling time estimate

Preliminary non-linear fits of the integrated form of Eq. 4 (needed to account for prey depletion; see below) yielded $h < 0$. This is incompatible with the biological meaning of this parameter. When constraining the parameter to be non-negative, the estimate of h was consistently 0. Moreover, the graphical representation of the observed functional response (Fig. 2) shows that predator saturation did not occur within the range of prey densities used in the experiments. This makes estimation of the parameter h mathematically impossible. Consequently, it is reasonable to set h to 0. This does not imply that the handling time is really zero but only expresses the fact that predator saturation does not occur in this data set. This assumption simplifies Eq. 4 to:

$$g(N, P) = \left(\alpha + \beta \frac{N}{P^m} \right) \frac{N}{P^m}. \quad (5)$$

In the rest of this work, we qualify as “type-III” responses all those with $\beta > 0$, even though Eq. 5 does not describe, strictly speaking, the type-III functional response as defined by Holling (1959) because of the absence of saturation. In the case that $\beta = 0$, Eq. 5 becomes a type-I model (and not a type-II because of the absence of the handling time).

Prey depletion

To account for prey depletion during a finite time interval $[t_1, t_2]$, the instantaneous rate of prey consumption $g(N, P)$ must be integrated over the period $[t_1, t_2]$ in order to predict the actual number of prey eaten during this time. It is this integrated form that must be fitted to the data. The integrated form is obtained by solving the differential equation

$$\frac{dN}{dt} = -g(N, P)P.$$

By using the model of $g(N, P)$ defined by Eq. 5, this yields:

$$N_2 = \begin{cases} \frac{N_1 P_1^{2m-1}}{P_1^{2m-1} + \beta N_1 T} & \text{if } \alpha = 0 \\ \frac{\alpha N_1 P_1^m}{(\alpha P_1^m + \beta N_1) \exp\left(\frac{\alpha T}{P_1^{m-1}}\right) - \beta N_1} & \text{if } \alpha \neq 0 \end{cases} \equiv f(N_1, P_1, T) \quad (6)$$

where $T = t_2 - t_1$ and P_1 is the predator density (assumed to remain constant between t_1 and t_2). The number of prey eaten during $[t_1, t_2]$ is thus $N_1 - N_2$.

Predator densities

As mentioned previously, for each experimental day followed by Schenk et al. (2005), an estimate of the number of wasps can be reconstructed in each of the ten hours of the activity period. Consequently, the relation between the final and the initial numbers of prey (respectively N_{11} and N_1) is given by the iterative relation:

$$N_{i+1} = f(N_i, P_i, 1) \quad \text{for } i = 1 \text{ to } 10 \quad (7)$$

with f the function defined by Eq. 6, N_i the number of prey alive at the beginning of the i th hour and P_i the number of active predators during the i th activity hour. The latter is obtained by multiplying the relative predator activity (in comparison with the 13–14 h value which is set to 1) for this time interval by M_c , the mean number of wasps caught during the 13–14 h slot either with open cages ($M_{1,2,3} = 3.708$) or without open cage ($M_0 = 1.75$).

Schenk et al. (2005) ignored the hourly variations of the predator density and used a constant value \tilde{P} over the day. If we make the same simplification, then the number of prey surviving at the end of an experimental day is given by:

$$N_{11} = f(N_1, \tilde{P}, 10) \quad (8)$$

with \tilde{P} the mean number of active predators during the ten activity hours. Schenk et al. (2005) estimated \tilde{P} as the sum of the densities in each hour:

$$\tilde{P} = \sum_{i=1}^{10} P_i. \quad (9)$$

Table 1. Set of candidate models. All models assume no handling time ($h = 0$). Models with $m = 1$ are ratio dependent; they are nested into equivalent predator dependent models with free m . Models with $\beta = 0$ are of type I; those with $\beta > 0$ are of type III. The parameter α gives more generality but turns out to be unnecessary when $\beta > 0$ (see text).

Model	Abundance of predators	No. free parameters	Functional response model
1	constant (\bar{P} , Eqs. 8 and 10)	3: m, β, α	$g(N, P) = (\alpha + \beta \frac{N}{\bar{P}}) \frac{N}{\bar{P}}$
7	variable (P_i , Eq. 7)		
2	constant (\bar{P} , Eqs. 8 and 10)	2: $\beta, \alpha; (m = 1)$	$g(N, P) = (\alpha + \beta \frac{N}{\bar{P}}) \frac{N}{\bar{P}}$
8	variable (P_i , Eq. 7)		
3	constant (\bar{P} , Eqs. 8 and 10)	2: $m, \beta, (\alpha = 0)$	$g(N, P) = \beta (\frac{N}{\bar{P}})^2$
9	variable (P_i , Eq. 7)		
4	constant (\bar{P} , Eqs. 8 and 10)	1: $\beta; (m = 1, \alpha = 0)$	$g(N, P) = \beta (\frac{N}{\bar{P}})^2$
10	variable (P_i , Eq. 7)		
5	constant (\bar{P} , Eqs. 8 and 10)	2: $m, \alpha; (\beta = 0)$	$g(N, P) = \alpha \frac{N}{\bar{P}}$
11	variable (P_i , Eq. 7)		
6	constant (\bar{P} , Eqs. 8 and 10)	1: $\alpha; (m = 1, \beta = 0)$	$g(N, P) = \alpha \frac{N}{\bar{P}}$
12	variable (P_i , Eq. 7)		

Obviously, this was an error and must be corrected to:

$$\tilde{P} = \frac{1}{10} \sum_{i=1}^{10} P_i. \quad (10)$$

This correction is of no consequence to the estimates of parameters that do not depend on the units of predator density. Particularly, it has no effect on m , which is the main parameter of interest.

In the present paper, we compare models using a constant predator density (\bar{P}) with models accounting for the variations during the 10 hours (P_i , $i = 1$ to 10) the latter making a better use of the available information about the wasp daily activity pattern. The set of candidate models is given in Table 1. Among these models, model 3 is the most similar to that used by Schenk et al. (2005). Differences between these two models are summarized in Table 2.

Parameter estimates

Non-linear regressions ($n = 32$) are performed with the *nls* function of the R software (R Development Core Team 2010). Graphs of residuals (not shown here) suggested that the

data do not fulfil the normality assumption. Consequently, a non-parametric bootstrap method is used to determine the confidence intervals of the parameter estimates. This method involves generation of new data sets by residual resampling. After fitting the model, fitted values and residuals are retained. New data sets are generated by adding a randomly chosen residual (with replacement) to each of the fitted values. For each of the 10,000 data sets generated in this way, we obtain new parameter estimates so that the distribution of model parameters can be reconstructed empirically. A confidence interval for each parameter can therefore be defined.

Model selection

In order to compare the models, the second order Akaike criterion (AIC_c) and the relative Akaike weight w_i are calculated for each candidate model. It is generally considered that models for which $\Delta_i \leq 2$ ($\Delta_i = AIC_i - AIC_{\min}$) have substantial support, models having Δ_i of about 4 to 7 have considerably less support, while models with $\Delta_i \geq 10$ have essentially no support and can be omitted from further consideration (Burnham and Anderson 1998).

Table 2. Comparison between the model used by Schenk et al. (2005) and model 3, which is the most similar but corrects a few unsupported assumptions. See text for further explanations.

Model	No. predators \bar{P}	h	β	m
Schenk et al. (2005)	Eq. 9	0.17†	0.0039†	free to adjust
This study, model 3	Eq. 10	0	free to adjust	free to adjust

† From Schenk and Bacher (2002).

Table 3. Parameter estimates after non-linear regression, and model ranking based on Akaike's criterion. Results for pure prey-dependent models ($m = 0$) are not shown as they all fit very poorly ($\Delta AIC_c > 20$) in comparison with predator- and ratio-dependent models. Two models are considered in a tie in ranking if the difference between their AIC_c is smaller than 1. Models 1, 3, 4 have the highest rank.

Model	m	β	α	AIC_c	rank	w_i
1	1.59 [1.11; 2.33]	0.0081 [0.0012; 0.025]	0.041 [0; 0.15]	182.04	1(tie)	0.2456
2	1	0.0053 [0.0010; 0.0081]	0.0094 [0; 0.60]	184.31	4(tie)	0.0789
3	1.44 [0.98; 2.19]	0.012 [0.0062; 0.044]	0	181.28	1(tie)	0.3599
4	1	0.0062 [0.0052; 0.0094]	0	182.29	1(tie)	0.2177
5	2.21 [1.62; 2.94]	0	0.16 [0.097; 0.27]	183.90	4(tie)	0.0972
6	1	0	0.068 [0.051; 0.084]	193.87	6	0.0007

Note: Values in square brackets are 95% CIs.

The Akaike weight w_i can be interpreted as the probability that model i is the best model for the observed data, given the set of candidate models (Johnson and Omland 2004). A confidence set of models can be obtained by summing the w_i from largest to smallest until that sum is just greater than a given probability that the best approximating model is contained within the confidence set (Burnham and Anderson 1998). As a complement, likelihood ratio tests (LRTs) are used to compare pairs of nested models. With respect to a “simple” model, the LRT provides a statistical criterion to assess the significance of the fitting improvement of a “richer” model that contains additional parameters. However, unlike AIC_c , LRTs cannot be used to test simultaneously all models in a candidate set and can only be applied to nested models (Burnham and Anderson 1998).

RESULTS

The fits of purely prey-dependent models (with $m = 0$) were clearly worse than fits of ratio-dependent and predator-dependent models ($\Delta AIC_c > 20$). Consequently, they are not presented and discussed thereafter.

Contrary to what was expected, using a constant number of predators over the whole activity period, thereby ignoring the variations of this number during the day is of no real consequence. The estimates of the parameter m as well as the AIC_c are identical when using either Eq. 7 or Eqs. 8 and 10 for the analyses.

Only the estimates of the other parameters are different. In fact, in the case in which the activity profile is the same on all experimental days, the estimate of the parameter m depends only on the average number of predators present during the day and not on the hourly variations of this number. This numerical finding can be proved analytically in special cases. Consequently, we can reduce the set of candidate models to models 1 to 6 (see Table 1).

Fitting results and Akaike criteria for predator-dependent and ratio-dependent models are shown in Table 3. Responses of type I (i.e., with $\beta = 0$; models 5 and 6) fit the data poorly. Model 6 is even the only model that fits clearly worse than the others ($\Delta AIC_c > 10$). Responses of type III ($\beta > 0$; models 1, 2, 3, and 4) fit better. This is also supported by the LRTs (Table 4): these tests show that the addition of the parameter β always improves the fits significantly ($p < 0.05$). Among type-III models, those with $\alpha = 0$ can be used with no significant loss of performance (LRT of model 3 vs. model 1: $p = 0.19$; LRT of model 4 vs. model 2: $p = 0.62$). According to the AIC_c ranking, three nested models (models 1, 3 and 4) can be considered as the best ones. As explained above, the LRT indicates that model 3 can be preferred to model 1. The 95% confidence interval of m in model 3 includes 1 (Table 3). Moreover the LRT of model 4 vs. model 3 (Table 4) indicates that the ratio-dependent model ($m = 1$) performs as well as the equivalent model with free m ($p = 0.0699$). These results lead therefore to the conclusion that the ratio-depen-

Table 4. Results of likelihood-ratio tests for pairs of nested models. Within the set of three best models that was selected by Akaike's criterion (models 1, 3, 4, Table 3), LRTs show that model 1 is less parsimonious than both 3 and 4, and that model 3 is less parsimonious than model 4, which is therefore the best choice.

Complex model	Simple model	LR	Additional parameters	df	p-value
1	2	4.72	m	1	0.02978*
	3	1.69	α	1	0.19401
	4	4.97	m, α	2	0.08322
	5	4.30	β	1	0.03804*
	6	16.56	m, β	2	0.00025***
2	4	0.25	α	1	0.61666
	6	11.83	β	1	0.00058***
3	4	3.29	m	1	0.06989
5	6	12.25	m	1	0.00046***

dent unsaturated type-III model (model 4) is the most parsimonious representation of the functional response of the wasp *P. dominulus* preying on *C. rubiginosa* (Fig. 2):

$$g(N, P) = \beta \left(\frac{N}{P} \right)^2. \quad (11)$$

DISCUSSION

It is generally difficult to monitor predation events in the field because of their secretive nature. However, the specific system that was set up by Schenk and Bacher (2002) has permitted to conduct in the field bivariate functional response experiments, i.e., to observe the number of prey eaten for various densities of both the prey and the predator populations. In their original analysis, Schenk et al. (2005) showed that predator interference occurred in *P. dominulus* and suggested that both direct (behavioural interactions) and indirect (non-random search for prey) mechanisms could be implicated. Moreover, they concluded that the functional response of *P. dominulus* was neither prey dependent nor ratio dependent, with both extremes clearly rejected. By re-analyzing the same data incorporating more realistic assumptions, we have shown here that the functional response of this predatory wasp can actually be considered as ratio dependent. Not only is the possibility of ratio dependence included in the confidence interval of the best-fitting model, but a ratio-dependent model fits as well as this best-fitting model in spite of a smaller number of parameters.

In artificial settings, the predator density can be controlled and is generally held constant. In

natural settings, the predator density may fluctuate during the interaction sessions. This can have consequences on the parameter estimates. However, we have shown here that this has no effect on the estimate of the mutual interference parameter m . It is sufficient to know the daily average of the predator density. Since m is the major parameter of interest, this property has a great practical interest.

In their original analysis, Schenk et al. (2005) did not estimate all functional response parameters from the same data set. The handling time h and the parameter β were taken from the observations of Schenk and Bacher (2002) ($h = 0.17 \pm 0.02$ h; $\beta = 0.0039 \pm 0.0005$). When conducted at another site (Schenk and Bacher 2002), experiments led again to quite different estimates of h (0.07 ± 0.01 h) and of β (0.0074 ± 0.001). Thus, these two parameters can change according to environmental conditions. Let us consider modifications of models 3 and 9 so as to re-incorporate the effect of a handling time (i.e., use Eq. 4 instead of Eq. 5). If we follow Schenk et al. (2005) by setting $h = 0.17$ and $\beta = 0.0039$, we find $m = 0.698$ with the modified model 3 and $m = 0.663$ with the modified model 9. These values are closer to the value obtained by Schenk et al. (2005) than to those obtained in the present study by estimating all parameters simultaneously. We can conclude that the "intermediate" value of m obtained by Schenk et al. (2005) is related to the fact that the various parameters had been estimated in separate experiments. While such procedure is sometimes unavoidable, the present data set is of sufficient quality to estimate all parameters simultaneously, thereby providing more reliable values.

Much theoretical work focusing on the impli-

cations of mutual interference for population dynamics has demonstrated its stabilizing effect in predator-prey systems. Although top-down effects are reduced in comparison with prey-dependent models, predators can still regulate the prey and check their outbreaks whether predator dependence is moderate ($m < 1$), ratio dependent ($m = 1$) or strong ($m > 1$) (Arditi and Berryman 1991, Berezovskaya et al. 2001, Arditi et al. 2004). Consequently, our re-evaluation of the mutual interference strength in *P. dominulus* does not mean that this predator cannot play a key role in the regulation of its prey *C. rubiginosa*. However, the study of the dynamics of this system is not the aim of the present work because the available data do not allow it: time series of freely reproducing populations would be necessary.

Our revised analysis of the 2005 experiment has shown that the handling time could be neglected in these data. This is due to the low prey densities used in this experiment. Schenk and Bacher (2002) had shown that the inflexion of the functional response due to the saturation effect of the handling time occurred at a prey density higher than 40, which is the highest value considered in the 2005 experiment. As we have already said, there is absolutely no sign of saturation in these data (Fig. 2), a situation that might also be amplified by the fact that wasp densities were much higher in the 2005 experiment (median wasp densities = 3 counts per hour) than in the 2002 experiment (median densities = 1 count per hour).

The main feature of the type-III functional response is the acceleration (convexity) at low prey densities. Our statistical analysis confirms this convexity, which was visually evident in Fig. 2, and which had previously been demonstrated by Schenk and Bacher (2002). This can be modelled with the searching efficiency being an increasing function of prey density. Schenk and Bacher (2002) had found a proportional relationship between the searching efficiency and the initial number of prey. We have considered here the actual number of available prey (our Eq. 3) rather than the initial number, which is more in line with the instantaneous concept of the functional response. As noted by Schenk and Bacher (2002), the acceleration of the predation rate at low prey densities could be due to the fact

that *P. dominulus* is a generalist predator. Tschanz et al. (2007) showed that prey switching between *C. rubiginosa* and larvae of flour beetles *Tenebrio molitor*, offered in an experiment as an alternative prey of *P. dominulus*, could not explain the type-III functional response, but they proposed alternative mechanisms, such as learning or the presence of still another prey than *C. rubiginosa* and *T. molitor*.

In the context of the debate over the ratio-dependent hypothesis, a number of experimental studies could be analyzed to support or reject this hypothesis (see Chapter 2 of Arditi and Ginzburg 2012). They all demonstrate predator dependence to various degrees and many of them provide support for ratio dependence as an acceptable approximation (DeLong and Vasseur 2011). However, the majority of these empirical data come from laboratory experiments, with spatial and temporal scales that pertain more to behaviour than to population dynamics. To the best of our knowledge, the present experiment is only the second that demonstrates so clearly a ratio-dependent functional response by direct measurements in a natural setting. The only other field study that we are aware of is the Isle Royale wolf-moose system studied by Vucetich et al. (2002) and Jost et al. (2005). Together, they provide evidence that ratio dependence is not a laboratory artefact and can arise in natural conditions. By contrast, as reviewed by Arditi and Ginzburg (2012), there does not exist a single study, whether performed in the lab or in the field, that has ever demonstrated pure prey dependence.

All the empirical evidence thus strongly suggests that it is time to abandon models with pure prey dependence for understanding predator-prey population dynamics. Instead, models incorporating predator dependence must always be considered. The only two existing field studies have demonstrated ratio dependence, which is a dimensionally and parametrically simpler form of predator dependence. Clearly, there is a need for more field studies.

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