

An experimental test of the nature of predation: neither prey- nor ratio-dependent

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Summary

1. There is a current debate about the appropriateness of prey-dependent vs. ratio-dependent functional responses in predator–prey models. This is an important issue as systems governed by these models exhibit quite different dynamical behaviour. However, the issue is not yet resolved on a theoretical basis, and there is a lack of experimental evidence in natural systems. We used a paper wasp–shield beetle system in a natural setting to assess the validity of either approach.
2. We manipulated the abundance of herbivorous insect prey on thistle plants and of predatory paper wasps in the immediate environment of the prey by opening or closing cages containing wasp nests.
3. The number of wasps foraging at the site increased when cages were opened, but rapidly reached an asymptote, indicating predator interference. The predation rate per predator decreased with the number of wasps in the environment. Thus, the functional response depended on both prey and predator density.
4. Neither a pure prey- nor a pure ratio-dependent model fitted perfectly our observations. However, the functional response of the paper wasps towards shield beetle larvae was closer to ratio-dependence. To our knowledge, this is the first experimental evidence discriminating between ratio- and prey-dependence in a natural setting with unconfined predators and prey.
5. Predator interference was most probably responsible for the specific form of the functional response found. We found indications that both direct (e.g. aggression) and indirect interference mechanisms (e.g. depletion of easy-to-find prey) were at work in our system. We conclude that predator density cannot be ignored in models of predator–prey interactions.

Key-words: *Cassida rubiginosa*, functional response, *Polistes dominulus*, predation rate, predator interference.

Introduction

Trophic relations play a major role in structuring natural communities, and probably largely determine local species abundance. Predator–prey interactions are thus one of the best-studied phenomena in ecology. However, conventional, prey-dependent population models coupling predator behaviour to community dynamics often fail to describe real communities

adequately, an obstacle which is overcome by ratio-dependent models (Arditi & Ginzburg 1989).

The rate of prey consumption by an average predator is known as the functional response and can be classified as (1) prey-dependent, when the response is a function of prey density alone or (2) predator-dependent, when both predator and prey density have an effect on the response (Abrams & Ginzburg 2000). Among predator dependent theories, ratio-dependence assumes that the functional response is a function of the ratio of prey over predators (Arditi & Ginzburg 1989). Ratio-dependent models have been suggested to describe adequately the functional response in most predator–prey systems under controlled conditions (Arditi &

Akçakaya 1990). However, there has been considerable debate concerning the relative merits and demerits of ratio- vs. prey-dependent behavioural responses (Arditi, Ginzburg & Akçakaya 1991; Abrams 1994; Gleeson 1994; Sarnelle 1994; Akçakaya, Arditi & Ginzburg 1995; Berryman, Gutierrez & Arditi 1995). The question underlying the debate is how predator population density influences the average predator's consumption rate.

This controversy has generated a large body of literature, but few studies measuring functional responses in natural settings (Abrams & Ginzburg 2000). We are aware of two intriguing exceptions: the wolf–moose system in Isle Royal National Park, Michigan, USA (Vucetich, Peterson & Schaefer 2002), and an experiment on predation by clerid beetles on a bark beetle species (Reeve 1997). In both studies, ratio-dependence accounted successfully for the observed rate of prey consumption, while prey-dependence was clearly rejected. However, this evidence rests on correlational data and semi-natural settings in which field cages restricted the movement of predators, respectively. Other studies, partly in natural settings, have attempted to discriminate models on the basis of statistical analyses of time-series, i.e. with observations of population densities alone, but without observation of the number of prey consumed (Jost & Arditi 2000, 2001; Jost & Ellner 2000). Results are not clear-cut but indicate that ratio-dependent functional responses may account for the observations. However, such studies are subject to alternative interpretation.

We determined recently the functional response of paper wasps, *Polistes dominulus* Christ (Hymenoptera: Vespidae), against larvae of the shield beetle, *Cassida rubiginosa* Müller (Coleoptera, Chrysomelidae) in the field by manipulating prey densities (Schenk & Bacher 2002). The paper wasps showed a sigmoid functional response (Holling Type III) at different study sites and in different years at constant predator densities. Considering the debate on ratio- vs. prey-dependent responses and the remaining lack of experimental field studies on this topic, our paper wasp–shield beetle system is a perfect setting to study the nature of predation in an unrestricted field situation. We determined the functional response of *P. dominulus* at one of the formerly used study sites, not only with varying prey densities but also with different predator densities. Here we report on the first such study in a completely natural setting. This allowed us not only to discriminate between prey- and ratio-dependence, but also to provide a sharper focus on the potential mechanisms underlying functional responses in the field.

Materials and methods

INSECT COLLECTION AND REARING

In May, shortly before the emerging phase, three nests of the paper wasp *P. dominulus* were collected in the

surroundings of Bern, Switzerland. The nests were glued to the interior top of three insect cages (50 × 50 × 80 cm). The cages were then attached to the west side of a greenhouse in the institute garden, where the experimental site is located. Cages were left open when no experiments were being conducted; otherwise, if the treatment required it, the cages were closed and the caged wasps were provided with water and honey water *ad libitum* and mealworms (*Tenebrio molitor* L.) according to the nest size. All wasps belonging to the same nest were colour-marked (acrylic colour, Waco). Marking was repeated every few days for newly emerged adults. Every experimental day nest sizes were determined. Fourth and early fifth instar larvae of *C. rubiginosa* used in the experiments were reared in the laboratory on cut shoots of creeping thistle.

EXPERIMENTAL SITE

The experiments were conducted in a natural 30 m² patch of approx. 200 creeping thistle *Cirsium arvense* (L.) Scop shoots, the host plants of *C. rubiginosa*. This patch was part of a larger, partly uncultivated meadow of about 1000 m² with a mixture of flowering plants, and was surrounded by orchard trees and hedges. The same patch was used in an earlier study on paper wasp predation towards *C. rubiginosa* (Schenk & Bacher 2002). All thistles were marked and numbered individually. The entire patch was searched for naturally occurring *C. rubiginosa* larvae, which were removed prior to the experiments. The identity of the predators was investigated by continuous video surveillance of individual beetle larvae as described in detail elsewhere (Schenk & Bacher 2002). In previous experiments we established that *C. rubiginosa* larvae will not disperse to plants other than creeping thistles, and that mortality from causes other than predation is virtually non-existent in late *C. rubiginosa* larval instars (S. Bacher unpublished). Thus, all missing larvae were attributed to predation. Predation recording took place from 3 June to 7 August 2002.

MEASURING PREDATOR RESPONSE

Treatments with different densities of prey and predators were conducted in a factorial design. Eight different densities of prey ($N = 2, 4, 6, 8, 10, 20, 30, 40$ larvae on the patch; the two last instars were used only) and four different densities of predators in the environment (no wasp cages open = natural wasp population density; one cage open; two cages open; three cages open = increased wasp densities) were tested. Experimental days were divided into blocks of four (each predator density) and prey densities were attributed randomly to the days, such that at the end of the experimental period each combination of prey and predator density had been investigated. Each morning the entire thistle patch was searched for all remaining larvae in order to determine the number of prey eaten the previous

day (ΔN). Early in the morning (before wasps started foraging) larvae were distributed on randomly selected thistles (determined by drawing numbers) of the patch and the required number of randomly selected cages was opened. Note that predator density was manipulated in the surrounding environment of the local site where prey was set and that the wasps were free to choose to forage on the site. In addition, every experimental day the number of predators foraging at the local site was determined during 1 h in the early afternoon (13–14 h), which corresponds to the peak activity of the wasps (Schenk & Bacher 2002); all predators observed foraging at the site were caught by sweep netting and released afterwards. Before release, all resident wasps caught (i.e. not belonging to one of the nests in the cages) were marked individually with acrylic colour. Experiments were not conducted on rainy days (no rainfall during the daily foraging period).

ANALYSES

We analysed our treatment effect (number of cages open) on predation rate with an ANCOVA, with the number of prey n as covariate. Predation rate was measured as the observed number of prey eaten (ΔN) divided by the estimated number of wasps at the local site during the day. Because we counted wasps during the hour of peak activity, the total number of wasps P for a given day d and a given number of cages open ($c = 0-3$) was estimated as follows: from a previous study (Fig. 1a in Schenk & Bacher 2002) we had an estimation of the activity of the wasps for each hour and were able to compute the percentage of wasps p_h expected to be found for a given hour h with respect to the modal interval ($h = 1-8$, with $h = 3$ the modal interval corresponding to the hour of the sampling, i.e. 13–14 h). Knowing w_d , the number of wasps caught between 13 h and 14 h (the modal interval), and M_c , the average number of wasps caught between 13 h and 14 h for a given number of open cages (see Fig. 1 in this paper), the expected total number of wasps for day d is:

$$P_d = \sum_{h=1}^2 p_h M_c + w_d + \sum_{h=4}^8 p_h M_c \quad \text{eqn 1}$$

Because the relationship between the number of prey and the predation rate was not linear, we used log-transformed rates of predation as the response variable in the ANCOVA.

We used the following approach to determine to what extent the observed rate of prey consumption fitted prey- or ratio-dependent models. From the results of a previous study (Schenk & Bacher 2002), we assumed the functional response of the wasp to be of Holling Type III (Hassell *et al.* 1977), with attack rate α as a linear function of prey density ($\alpha = bN$). We used the method of Arditi & Saïah (1992) for discriminating between a prey- and ratio-dependent functional response, adapted for a Type III response. The functional response g was modelled as:

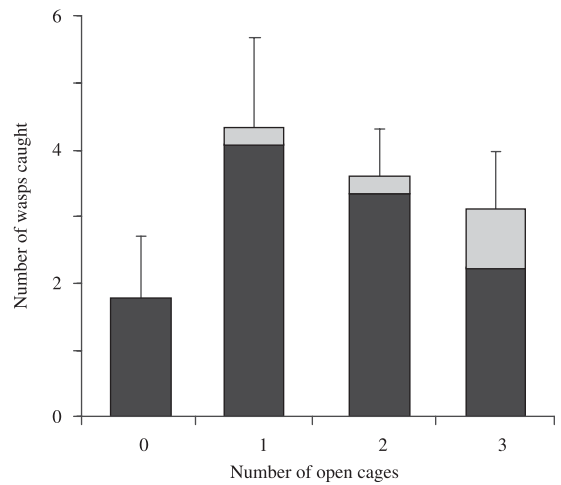


Fig. 1. Mean number of wasps caught between 13 h and 14 h with different numbers of cages open. Grey bars indicate the mean number of wasps originating from the nests in the cages; black bars show the mean number of resident wasps caught. Standard errors are shown for the total number of wasps caught.

$$g(N, P) = \frac{b \left(\frac{N}{P^m} \right)^2}{1 + b t_h \left(\frac{N}{P^m} \right)} \quad \text{eqn 2}$$

with m a fitted parameter that takes the value 0 for pure prey-dependence and 1 for pure ratio-dependence. To account for prey depletion during the course of the experiment, the instantaneous rate of prey consumption $g(N, P)$ must be integrated over the finite time period of the experiment T in order to yield the actual number of prey eaten ΔN , which is given by:

$$\Delta N = \frac{P^{2m} + bN^2 t_h + bNPT \pm \sqrt{-4b^2 N^3 P t_h T + (P^{2m} + bN^2 t_h + bNPT)^2}}{2bN t_h} \quad \text{eqn 3}$$

with N the number of shield beetles at the start of each experimental day, P the total number of wasps found during the course of the day, which was estimated by eqn 1, and T the time during which wasps forage, i.e. 8 h. We set $b = 0.004$ and handling time $t_h = 0.17$ from the results found in the earlier experiment (see Table 3 in Schenk & Bacher 2002). The parameter m was estimated by non-linear regression, using the sequential quadratic algorithm of SPSS (version 11.5), and standard error was obtained by a bootstrap procedure. Note that we assumed a constant number of wasps during the day. This was performed for computational simplicity, as using variable numbers of wasps would require integration over each hour of the day, with the additional complication of extrapolating the number of wasps present at each hour of the experiment. Such a stepwise integration would, moreover, require using the model to estimate the number of prey present at each hour. We are aware that other types of functional

responses can be used to analyse our results (e.g. Yodzis 1994; Vucetich *et al.* 2002). However, we restricted ourselves to the type III functional response for consistency with the earlier finding that it describes our system adequately (Schenk & Bacher 2002) and to avoid over-fitting (Ginzburg & Jensen 2004).

Results

Analysis of videotapes confirmed that 98% of predators ($n = 79$) were indeed *P. dominulus*. We checked that our treatment (opening cages) had an effect on the number of wasps foraging at the experimental site during the course of the experiment (ANCOVA with experimental date as covariable, $P = 0.001$) and that our treatment was randomized correctly during the course of the experiment (no significant relationship between experimental date and the number of cages open, the prey density, or the number of wasps caught at the local site; Kendall's τ , $P = 0.87, 0.58, \text{ and } 0.09$, respectively). The mean proportion of prey eaten during one experimental day was 46%, and was not correlated with N (Pearson's $r = 0.04$, $P = 0.81$).

We detected no significant difference between the number of wasps caught at the experimental plot when zero, one, two or three cages were open (Kruskal–Wallis test, $P = 0.18$; Fig. 1), but a significant increase in the number of wasps caught when at least one cage was open (Mann–Whitney U -test, $P = 0.031$). This difference was due mainly to resident wasps (Kruskal–Wallis test, $P = 0.067$). It appears that releasing additional predators in the environment increased their number at the local site, but that a maximum density was already reached with just one additional nest, suggesting predator interference. The number of larvae eaten per predator was expectedly dependent on the prey density (ANCOVA, $P < 0.001$; Fig. 2) as well as on the number of open cages (ANCOVA, $P = 0.006$, $R_{adj}^2 = 0.77$). Using either the total number of cages open ($P < 0.006$, R_{adj}^2

$= 0.77$) or the fact that a cage was open or not ($P < 0.001$, $R_{adj}^2 = 0.78$), we detected a clear effect of the treatment 'cage'; in other words, the density of the predators significantly affected the functional response of the wasps, being less efficient when more abundant.

The estimation of the parameter m allowed us to assess the extent to which our observations fit the prey- or the ratio-dependent model. The result of the non-linear regression yielded $m = 0.502$ ($n = 32$; $R_{adj}^2 = 0.67$; SE = 0.047; 95% confidence interval 0.40–0.61), indicating that the functional response of our system lies between prey- and ratio-dependence (Fig. 3a). However, the form of the fitted surface is much closer to ratio- than to prey-dependence (Fig. 3b). The estimate of m was robust to the use of different plausible values for b and t_h (from $m = 0.44$ with $b = 0.003$ and $t_h = 0.25$, to $m = 0.65$ with $b = 0.008$ and $t_h = 0.017$). In sum, the density of predators clearly affected their functional response, and prey-dependence is clearly rejected. The shape parameter m does not include one in its 95% confidence interval, indicating that our wasp-shield beetle system does not follow pure ratio-dependence. However, ratio-dependence is very close to our experimental results, and it represents a viable alternative in predator–prey models.

Discussion

To our knowledge, our study provides the first experimental evidence discriminating between ratio- and prey-dependence in a natural setting with unconfined predators and prey. Our finding of an intermediate form of the functional response in paper wasps corroborates the prediction that both precise prey-dependence and ratio-dependence are rare in nature (Abrams & Ginzburg 2000). However, while prey-dependence is rejected unambiguously, our observations are close to ratio-dependence. Thus, the latter model may provide an acceptable description of our system.

As postulated by ratio-dependent theory, predator interference is most probably responsible for the specific form of the functional response found. Predator interference in the field arises from direct behavioural interactions, e.g. aggression. The appearance of predator interference can also be caused indirectly, first via the effect of non-random search for prey (Free, Beddington & Lawton 1977), and secondly because of natural variation in the vulnerability of prey to predators in any heterogeneous environment, i.e. in most natural systems (Abrams 1994). As prey are depleted during the course of an experiment, the average vulnerability of the remaining individuals decreases, and predators are less and less efficient. We have indications that both direct and indirect mechanisms are at work in our system. First, the observation that wasp densities attain an asymptote at the local site suggests that *P. dominulus* cannot fill the space available without bounds. Moreover, the fact that the increase of wasp density was due to resident wasps indicates that these wasps

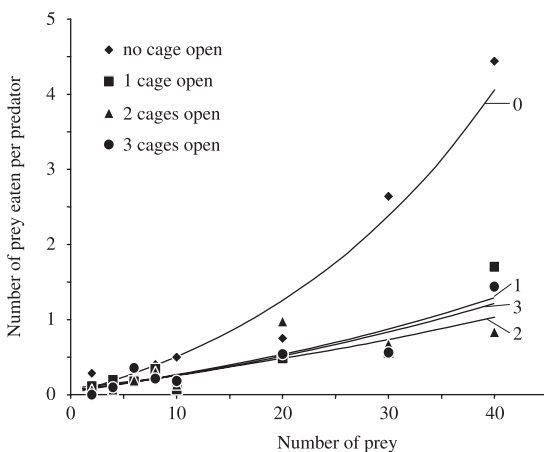


Fig. 2. Number of prey eaten per predator at different prey densities, when zero, one, two or three cage(s) were open, and fitted curves. The treatment (opening cages) had a significant effect on predation rate.

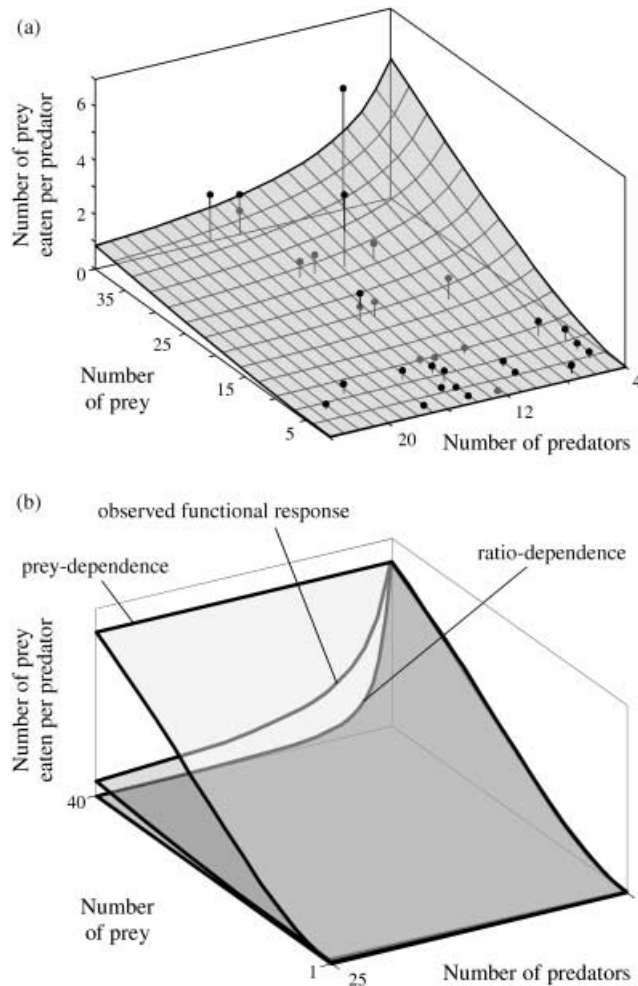


Fig. 3. (a) Number of prey eaten per predator as a function of prey and predator numbers, and fitted surface. The observations (circles) show an intermediate form of the functional response between prey- and ratio-dependence. (b) Comparison of the observed functional response with prey- and ratio-dependence. Note that the observed functional response is much closer to ratio- than to prey-dependence.

were expelled from their normal foraging places and switched to the experimental site. In addition, there was a decrease in the predation rate when opening cages. Both observations indicate direct behavioural interference between the wasps. We believe that this simple form of direct predator interference for space (foraging sites) was the probable reason for wasps being less efficient predators when foraging at high densities, having to cope with a higher number of competitors in the environment. Thus, the experimental area constituted a competitor-free space for the resident wasps. Secondly, distributing larvae in our experiment on randomly selected host plants caused an unequal probability of being eaten for individual larvae, because some larvae were placed on thistles more hidden in the vegetation (where predation rates are lower) and others were placed on thistles exposed to the predators (where predation rates are higher; Tschanz & Bacher, unpublished). Apparently, these two mechanisms led to a functional response approaching ratio-dependence in our study. Repeating the experiment

described here with a homogeneous prey distribution (e.g. by distributing the larvae on standardized artificial plants), thus eliminating apparent predator interference via prey depletion, may reveal the importance of indirect effects in creating intermediate functional responses as opposed to other types of predator-dependence. Experiments in this and other natural systems on the precise mechanisms of predation are greatly needed to advance our understanding of the form of particular functional responses. If we understand better the mechanisms causing predator-dependence we can probably solve the controversy about which form of the functional response to use when modelling predator-prey interactions.

Our study demonstrated that predator density cannot be ignored in models of predator-prey interactions. However, more studies on predator-dependent functional responses in other predator-prey systems are necessary before we can make generalizations about the importance of predator interference for predator-prey dynamics in natural systems.

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References

- Abrams, P.A. (1994) The fallacies of 'ratio-dependent' predation. *Ecology*, **75**, 1842–1850.
- Abrams, P.A. & Ginzburg, L.R. (2000) The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology and Evolution*, **15**, 337–341.
- Akçakaya, H.R., Arditi, R. & Ginzburg, L.R. (1995) Ratio-dependent predation: an abstraction that works. *Ecology*, **76**, 995–1004.
- Arditi, R. & Akçakaya, H.R. (1990) Underestimation of mutual interference of predators. *Oecologia*, **83**, 358–361.
- Arditi, R. & Ginzburg, L.R. (1989) Coupling in predator–prey dynamics: ratio dependence. *Journal of Theoretical Biology*, **139**, 311–326.
- Arditi, R., Ginzburg, L.R. & Akçakaya, H.R. (1991) Variation in plankton densities among lakes – a case for ratio-dependent predation models. *American Naturalist*, **138**, 1287–1296.
- Arditi, R. & Saïah, H. (1992) Empirical evidence of the role of heterogeneity in ratio-dependent consumption. *Ecology*, **73**, 1544–1551.
- Berryman, A.A., Gutierrez, A.P. & Arditi, R. (1995) Credible, parsimonious and useful predator–prey models – a reply. *Ecology*, **76**, 1980–1985.
- Free, C.A., Beddington, J.R. & Lawton, J.H. (1977) Inadequacy of simple-models of mutual interference for parasitism and predation. *Journal of Animal Ecology*, **46**, 543–554.
- Ginzburg, L.R. & Jensen, X.J. (2004) Rules of thumb for judging ecological theories. *Trends in Ecology and Evolution*, **19**, 121–126.
- Gleeson, S.K. (1994) Density dependence is better than ratio dependence. *Ecology*, **75**, 1834–1835.
- Hassell, M.P., Lawton, J.H. & Beddington, J.R. (1977) Sigmoid functional response by invertebrate predators and parasitoids. *Journal of Animal Ecology*, **46**, 249–262.
- Jost, C. & Arditi, R. (2000) Identifying predator–prey processes from time-series. *Theoretical Population Biology*, **57**, 325–337.
- Jost, C. & Arditi, R. (2001) From pattern to process: identifying predator–prey models from time-series data. *Population Ecology*, **43**, 229–243.
- Jost, C. & Ellner, S. (2000) Testing for predator dependence in predator–prey dynamics: a non-parametric approach. *Proceedings of the Royal Society of London B*, **267**, 1611–1620.
- Reeve, J.D. (1997) Predation and bark beetle dynamics. *Oecologia*, **112**, 48–54.
- Sarnelle, O. (1994) Inferring process from pattern: trophic level abundances and imbedded interactions. *Ecology*, **75**, 1835–1841.
- Schenk, D. & Bacher, S. (2002) Functional response of a generalist insect predator to one of its prey species in the field. *Journal of Animal Ecology*, **71**, 524–531.
- Vucetich, J.A., Peterson, R.O. & Schaefer, C.L. (2002) The effect of prey and predator densities on wolf predation. *Ecology*, **83**, 3003–3013.
- Yodzis, P. (1994) Predator–prey theory and management of multispecies fisheries. *Ecological Applications*, **4**, 51–58.