

# Functional responses modified by predator density

Pavel Kratina · Matthijs Vos · Andrew Bateman ·  
Bradley R. Anholt

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**Abstract** Realistic functional responses are required for accurate model predictions at the community level. However, controversy remains regarding which types of dependencies need to be included in functional response models. Several studies have shown an effect of very high predator densities on per capita predation rates, but it is unclear whether this predator dependence is also important at low predator densities. We fit integrated functional response models to predation data from 4-h experiments where we had varied both predator and prey densities. Using an information theoretic approach we show that the best-fit model includes moderate predator dependence, which was equally strong even at low predator densities. The best fits of Beddington–DeAngelis and Arditi–Akçaya functional responses were closely followed by the fit of the Arditi–Ginzburg model. A Holling type III functional response did not describe the data well. In addition, independent behavioral observations revealed high encounter rates between predators. We quantified the number of encounters between predators and the time the focal predator spent interacting with other individuals per encounter. This time “wasted” on conspecifics reduced the total time available for foraging and may therefore account for lower predation rates at higher predator densities. Our

findings imply that ecological theory needs to take realistic levels of predator dependence into account.

**Keywords** Consumer–resource interactions · Food web · Interference · Experimental microcosms · Prey depletion

## Introduction

Food webs are descriptive devices defined by the linkages between consumers and their resources. These systems are extraordinarily complex and intrinsically dynamic. Functional responses are central components of community and food web models and their mathematical forms strongly influence the dynamics and stability of ecological systems (May 1973; Oaten and Murdoch 1975; Vos et al. 2001; Gross et al. 2004; McCann et al. 2005). A consumer’s functional response is a function of resource density (Solomon 1949; Holling 1959, 1966). However, it has been shown that other species and other predators can directly or indirectly alter the process of predation. Whether these interactions need to be incorporated into food web models and how exactly they affect the shape and the magnitude of functional responses are still poorly understood.

It has been previously demonstrated that foraging success of consumers declines with increasing diversity of resources (Hillebrand and Cardinale 2004), perhaps because consumers become less efficient when the density and diversity of species not included in their diet increase (Vos et al. 2001; Grabowski 2004; Kratina et al. 2007). Functional responses can be further modified by the presence of other consumers. Additional predators can either facilitate predation, as in group hunting (e.g., lions), or more often interfere with the ability of a focal predator to successfully find and capture prey (Salt 1967, 1974; Arditi

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P. Kratina (✉) · A. Bateman · B. R. Anholt  
Department of Biology, University of Victoria,  
P.O. Box 3020, Victoria, BC V8W 3N5, Canada  
e-mail: pavelk@uvic.ca

M. Vos  
Centre for Estuarine and Marine Ecology,  
Netherlands Institute of Ecology (NIOO-KNAW),  
P.O. Box 140, 4400 AC Yerseke, The Netherlands

and Akçakaya 1990; Osenberg et al. 1999). Many mechanisms have been proposed that can generate a predator-dependent consumption rate of individual predators. For example, predator dependence may arise from group formation, spatial distribution (Cosner et al. 1999) or strong social interactions among predators (Abrams and Ginzburg 2000). Other processes may include aggressive behavior resulting from population size structure and cannibalistic interactions (Crowley and Martin 1989; Crumrine 2005; Rudolf 2006, 2007).

Logistical considerations have constrained many previous empirical studies of predator dependence to not vary predator and prey densities together and to do so only over a restricted range of densities (Salt 1974; Crowley et al. 1987; Crowley and Martin 1989; Mills and Laca 2004). Often they used relatively few predator densities and compared the per capita consumption rates of the different densities to each other (but see Fussmann et al. 2005; Schenk et al. 2005). Some studies inferred predator dependence indirectly from time series data (Jost and Arditi 2000, 2001; Jost and Ellner 2000) or the direct experiments failed to account for the depletion of resources over the course of the experiments (e.g., Salt 1974; Hayward and Gallup 1976; Helgen 1987; Crowley and Martin 1989; Hansson et al. 2001; Lüring et al. 2003). Very few studies measured functional responses directly on a demographic time scale and accounted for prey depletion in their analysis. Among such rare exceptions that investigated predator dependence in natural populations are the studies by Vucetich et al. (2002), Jost et al. (2005) and Griffen and Delaney (2007).

Three distinct classes of functional response models have been traditionally used to analyze predator–prey data. Classic “prey-dependent” models assume that the predation rate is a function of only prey density (Holling 1959). Because intraspecific interactions between individual predators can affect predator efficiency, “predator-dependent” models estimate the predation rates that depend on densities of both prey and predator (Beddington 1975; DeAngelis et al. 1975). “Ratio-dependent” models are a special case of predator dependence where predation rate does not depend on absolute numbers of either species but only on the prey to predator ratio (Arditi and Ginzburg 1989). Which models should be used for predicting predator–prey or food web dynamics remains controversial (Abrams and Ginzburg 2000; Fussmann et al. 2005, 2007; Jensen et al. 2007).

There is no general agreement on the appropriate time scale of experimental studies. Feeding experiments that are nearly instantaneous relative to the generation times of model organisms are criticized for detecting only physical interference and failing to capture the interference caused by chemicals or inducible defenses (Arditi and Ginzburg 1989; Jensen et al. 2007). Conversely, longer-term studies

without prey replacement will give the appearance of predator dependence due to faster resource depletion in treatments with higher predator densities (Arditi and Saïah 1992; Abrams 1994). Although predator dependence is expected to arise at extremely high densities of predators (Abrams and Ginzburg 2000; Fussmann et al. 2005) it is still unclear whether functional responses remain predator dependent at low predator densities.

In contrast to most previous empirical studies, we aimed to directly estimate the effect of predator dependence on the detailed shape and magnitude of the functional response while simultaneously varying both the predator and prey densities over a large range. We investigated the functional response of the flatworm *Stenostomum virginianum* (hereafter predator or *Stenostomum*) feeding on its prey *Paramecium aurelia* (hereafter prey or *Paramecium*). Our major novel contribution was to determine whether the inclusion of predator dependence in the functional response model improves our description of predation at low predator densities. Furthermore, using an information theoretic approach, we directly compared the fits of three different model classes (prey dependent, ratio dependent, and predator dependent) to the same data set. We used integrated functional response models to account for the decline in prey density over the course of the 4-h experiment (Royama 1971; Rogers 1972; Juliano 2001).

In addition, we conducted a separate experiment wherein we measured and compared the encounter rate of focal predators with conspecifics over a range of predator densities and estimated the time that predators spend interacting with each other. Based on the results of both experiments and fitting models which either included or excluded predator dependence, we conclude that predation in this system is predator dependent even at relatively low predator densities.

## Materials and methods

### Model organisms and functional response experiment

We measured the per capita ingestion rate of the benthic flatworm *Stenostomum virginianum* (Rhabdocoela, Turbellaria) feeding on its prey *Paramecium aurelia* (Ciliophora) in experimental microcosms where we manipulated the densities of both predator and prey. Both species were originally isolated from sediments of freshwater ponds on the University of Victoria campus and maintained as asexually reproducing cultures since then.

We randomly assigned treatment combinations of predator and prey densities into 24-well tissue culture plates. We set prey densities at 60, 160, and 200 individuals in 900  $\mu$ l of the protozoan medium. Although we always pipetted low

(one) medium (nine), and high (19) numbers of *Stenostomum* into each treatment, some individuals were lost during the transfer (due to strong affinity of flatworms to the pipette tips). This resulted in an almost continuous distribution of predator experimental densities between one and 19 individuals per 900  $\mu\text{l}$ . Actual numbers of predators were counted at the end of the experimental period. The culture medium was prepared by filtering 1.5 crushed protozoan pellets ( $\sim 0.7$  g each; no. 13-2360; Carolina Biological Supply Company, N.C.) through double-layered no. 4 coffee filters and dissolved in 2 l of NAYA water. We measured the number of *Paramecium* eaten per predator in 4 h. This is an intermediate time frame between instantaneous predation rate measurements and the animal’s generation time (48–72 h). Predation was terminated by the addition of two drops of 5% acid Lugol’s solution and all individuals of both species were counted under a dissecting microscope (Leica MZ8).

Data analyses

We used sigmoid functional response models for our analyses as we have previously demonstrated that predatory *Stenostomum* forages on its prey with a Holling type III functional response (Altwegg et al. 2006; Kratina et al. 2007). Because it was logistically impossible to replace

mechanistic (Beddington–DeAngelis and Holling type III) to phenomenological (Arditi–Akçakaya and Arditi–Ginzburg) functional responses that are not nested and cannot be compared using likelihood ratios. The integrated form of the Beddington–DeAngelis type III model has not been previously used to analyze ecological data.

In order to estimate the influence of predator interference at low predator densities we also performed the fitting procedure for a data subset of only one to five *Stenostomum* predators per 900  $\mu\text{l}$ .

1. Arditi–Akçakaya functional response

The original model (Arditi and Akçakaya 1990) that distinguishes between prey dependence and ratio dependence was modified to type III (see Schenk et al. 2005):

$$f(N, P) = \frac{a\left(\frac{N}{Pm}\right)^2}{1 + ah\left(\frac{N}{Pm}\right)^2}$$

where  $N$  is the prey density at the start of the experiment,  $P$  the predator density,  $f$  the ingestion rate (number of prey eaten per predator per unit time),  $m$  the interference coefficient (this parameter is 0 for pure prey-dependence and 1 for pure ratio-dependence),  $a$  the encounter rate, and  $h$  the handling time.

When integrated to allow for prey depletion we have:

$$\Delta N = \frac{P^{2m} + ahN^2 + PaTN - \sqrt{(P^{2m} + ahN^2 + PaTN)^2 - 4TPha^2N^3}}{2ahN}$$

each consumed prey during the experiment, we accounted for depletion by integration of the functional response models (Royama 1971; Rogers 1972; Juliano 2001). To discriminate between predator dependence, ratio dependence, or prey dependence and estimate whether an increasing density of predators negatively affects per capita consumption rate, we fit four functional response models to the data: a modified form of the Beddington–DeAngelis model that incorporates interference as time spent during encounters with other predators, a modified form of the

where  $\Delta N$  is the number of prey eaten and  $T$  the duration of the experiment (the unit of time here  $T = 4$  h).

2. Beddington–DeAngelis functional response

The original predator-dependent model (Beddington 1975; DeAngelis et al. 1975) was modified to type III:

$$f(N, P) = \frac{aN^2}{1 + bw(P - 1) + ahN^2}$$

and then integrated to give:

$$\Delta N = \frac{(1 + i(P - 1)) + haN^2 + PTaN - \sqrt{((1 + i(P - 1)) + haN^2 + PaTN)^2 - 4TPha^2N^3}}{2Nha}$$

Arditi–Akçakaya model, a pure ratio-dependent Arditi–Ginzburg model, and a pure prey-dependent Holling type III model. The use of a model selection approach (Burnham and Anderson 2002) allowed comparison of

The parameters are the same as in the previous model, but predator dependence is modeled as  $i = bw$ , where  $b$  is the rate of encounter with other predators (analogous to the encounter rate with prey  $a$ ), and  $w$  is the time wasted on

other predators (analogous to  $h$  spent on each prey item). Because these two parameters are mathematically indistinguishable (they always appear together in the model) we grouped them into one parameter  $i$ .

### 3. Arditi–Ginzburg functional response

The original ratio-dependent model (Arditi and Ginzburg 1989) was modified to type III:

$$f(N, P) = \frac{a\left(\frac{N}{P}\right)^2}{1 + ah\left(\frac{N}{P}\right)^2}$$

and integrated to give:

$$\Delta N = \frac{P^2 + ahN^2 + PaTN - \sqrt{(P^2 + ahN^2 + PaTN)^2 - 4TPha^2N^3}}{2ahN}$$

### 4. Holling type III functional response

The original prey-dependent model (Holling 1959):

$$f(N) = \frac{aN^2}{1 + ahN^2}$$

was integrated to give:

$$\Delta N = \frac{ahN^2 + PaTN - \sqrt{(ahN^2 + PaTN)^2 - 4TPha^2N^3}}{2ahN}$$

All functional response models were fit to the observed data using nonlinear least-squares regression (Juliano 2001). We used the function `nls` in R software, version 2.6.0 (R Development Core Team 2007) and compared the explanatory power of the models using the sample size-adjusted Akaike's information criterion (AICc) (Burnham and Anderson 2002).

### Behavioral experiment

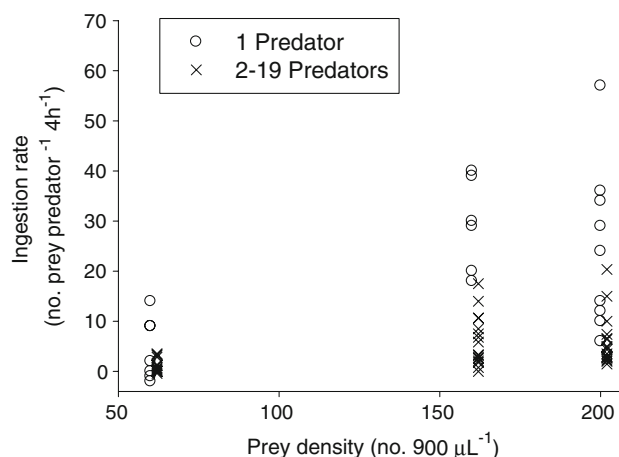
In a separate experiment we examined the number of encounters between the focal predator and its conspecifics. We visually monitored the focal predator in 9-well Pyrex depression plates with 900  $\mu\text{l}$  of the protozoan medium (see above) over 20 min. Our treatments consisted of 60 *Paramecium* and 2, 4, 8, or 16 *Stenostomum* per experimental well. All treatments were replicated 6 times. Stronger illumination from the microscope in the behavioral trials as compared to the functional response trials caused different light condition in the two experiments. We compared the fits of linear, hyperbolic, and sigmoid models and based on the smallest AIC value, we used the

hyperbolic function  $y = \frac{a(P-1)}{1+ab(P-1)}$  to analyze the predator encounter data. The number of encounters is denoted as  $y$ ,  $a$  and  $b$  are constants that can be interpreted as the encounter rate with conspecific predators and the time spent per encounter, respectively. The term  $(P - 1)$  ensures that the focal predator cannot interfere with itself.

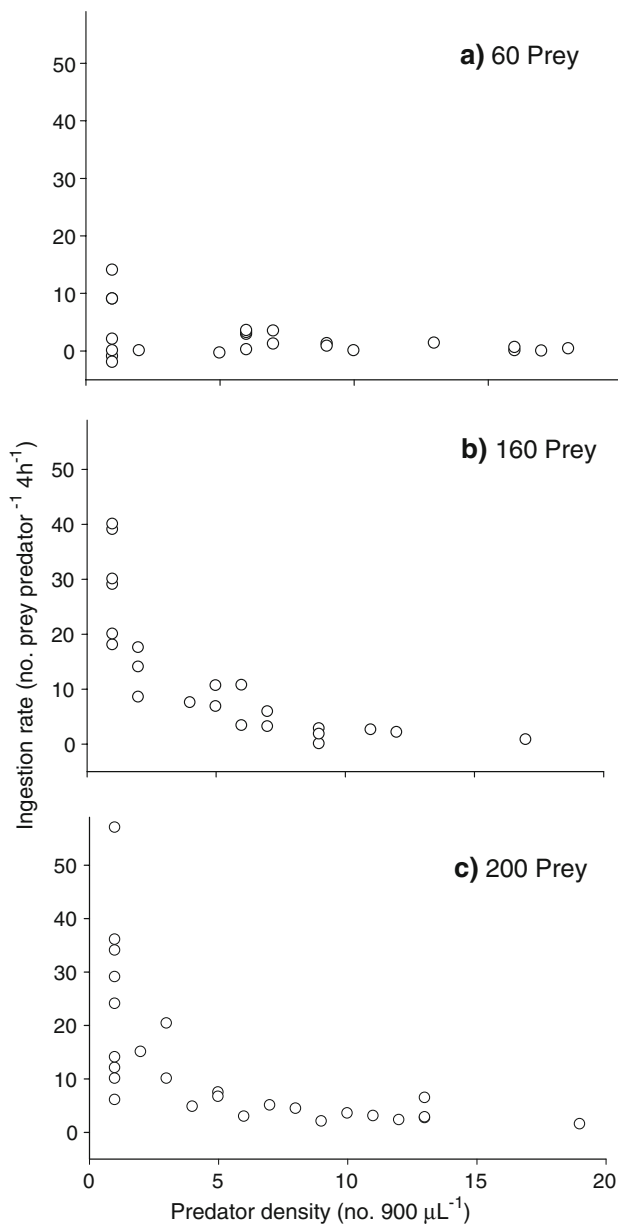
## Results

Predator per capita ingestion rate declined with increasing density of conspecifics and this effect was evident especially at high prey densities of 160 and 200 *Paramecium*

per experimental well (Figs. 1, 2). The Arditi–Akçakaya and Beddington–DeAngelis functional responses produced almost identical fits to our data (Fig. 3a, b; Table 1). The estimated parameters of both models were also very similar; with  $a = 6.7 \times 10^{-4}$  and  $h = 0.11$  in the Arditi–Akçakaya model and  $a = 8.4 \times 10^{-4}$  and  $h = 0.11$  in the Beddington–DeAngelis model. Both models also detected



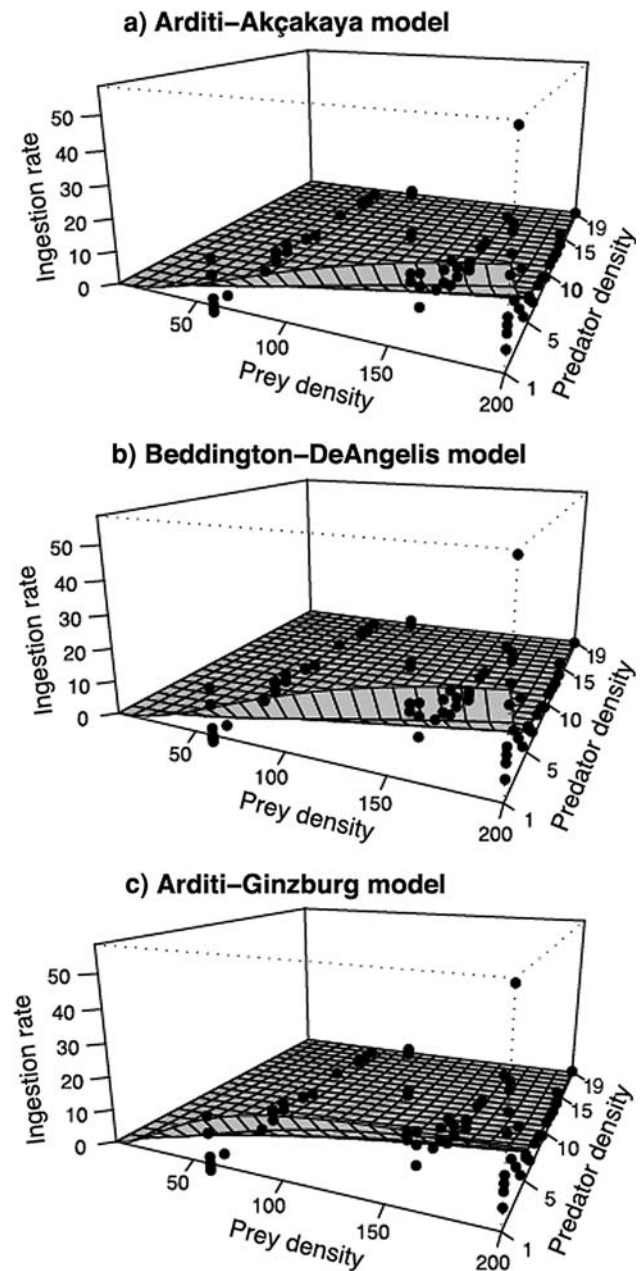
**Fig. 1** Per capita ingestion rate by predatory *Stenostomum* feeding on *Paramecium* for 4 h at three prey densities: 60 (23 replicates), 160 (22 replicates), and 200 (26 replicates) per 900  $\mu\text{l}$  of protozoan medium. Empty circles represent the treatment where the predator was feeding without conspecifics (i.e., one predator), crosses the treatment where predator density ranged from two to 19 *Stenostomum* in 900  $\mu\text{l}$  of protozoan medium. The three negative values of the predator ingestion rate at the lowest prey density resulted either from inaccurate pipetting or from *Paramecium* fission during the experiment. Individual symbols represent results of all replicates



**Fig. 2** Per capita ingestion rate of *Paramecium* by predatory *Stenostomum* over a range of one to 19 predator densities while feeding for 4 h on three prey densities: **a** 60, **b** 160 and **c** 200 *Paramecium* per 900  $\mu\text{l}$  of protozoan medium

a substantial level of predator interference;  $m = 0.67 \pm 0.11$  (SE) and  $i = 2.77 \pm 2.56$  (SE). The fits of the two best functional responses were closely followed by the fit of Arditi–Ginzburg functional response (AICc = 581.5; Table 1). The Holling type III model without the effect of conspecific density produced the worst fit (AICc = 622.6) and a negative handling time that is not biologically sensible (Table 1).

To assess whether the functional response is affected by conspecifics also at low densities, we repeated this analysis on a subset of the data with only one to five predators per



**Fig. 3** The three integrated type III functional response models, representing the effect of changing predator and prey densities on the per capita ingestion rate. **a** Arditi–Akçakaya model [encounter rate ( $a$ ) =  $6.7 \times 10^{-4}$ , handling time ( $h$ ) = 0.11, interference coefficient ( $m$ ) = 0.67], **b** Beddington–DeAngelis model [ $a = 8.4 \times 10^{-4}$ ,  $h = 0.11$ , predator interference ( $i$ ) = 2.77], **c** Arditi–Ginzburg model ( $a = 2.9 \times 10^{-3}$ ,  $h = 0.18$ ). The Holling type III functional response did not converge to an acceptable fit due to the negative handling time. Ingestion rate was measured as the number of prey consumed per predator per 4 h; predator and prey densities were measured as number of individuals per 900  $\mu\text{l}$  of protozoan medium

experimental well. We obtained very similar parameter estimates and model order as for the whole data set. The interference parameters were  $m = 0.66 \pm 0.23$  (SE) and

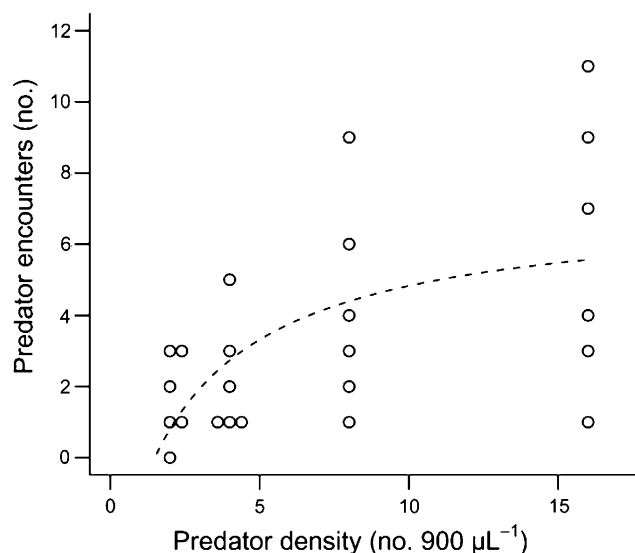
**Table 1** The parameter estimates ( $\pm 1$  SE) and summary of model selection analysis for the fits of four functional response models to the complete data set and to the data for low predator densities (one to five predators)

Model	Encounter rate	Handling time	Interference parameter	$K$	AICc <sup>a</sup>	$\Delta$ AICc <sup>b</sup>
Complete data						
Beddington–DeAngelis	$8.4 \times 10^{-4} \pm 7.6 \times 10^{-4}$	$0.11 \pm 0.04$	$i = 2.77 \pm 2.56$	3	576.0	0.8
Arditi–Akçakaya	$6.7 \times 10^{-4} \pm 3.4 \times 10^{-4}$	$0.11 \pm 0.04$	$m = 0.67 \pm 0.11$	3	575.2	0.0
Arditi–Ginzburg	$2.9 \times 10^{-3} \pm 0.4 \times 10^{-3}$	$0.18 \pm 0.03$	–	2	581.5	6.3
Holling type III	$7.6 \times 10^{-6} \pm 2.7 \times 10^{-6}$	$-3.46 \pm 1.39$	–	2	622.6	47.4
Data (1 – 5 predators)						
Beddington–DeAngelis	$7.7 \times 10^{-4} \pm 6.6 \times 10^{-4}$	$0.11 \pm 0.04$	$i = 2.06 \pm 1.85$	3	289.1	0.0
Arditi–Akçakaya	$6.6 \times 10^{-4} \pm 4.9 \times 10^{-4}$	$0.11 \pm 0.05$	$m = 0.66 \pm 0.23$	3	289.3	0.2
Arditi–Ginzburg	$1.7 \times 10^{-3} \pm 0.4 \times 10^{-3}$	$0.14 \pm 0.02$	–	2	289.9	0.8
Holling type III	$7.6 \times 10^{-5} \pm 4.5 \times 10^{-5}$	$-0.13 \pm 0.26$	–	2	307.8	18.7

$K$  Number of parameters,  $m$  interference coefficient,  $i$  predator interference

<sup>a</sup> A lower adjusted Akaike's information criterion (AICc) value indicates a superior model

<sup>b</sup>  $\Delta$ AICc shows the difference from the best model (in *italics*)



**Fig. 4** Behavior of the focal *Stenostomum* predator with 60 *Paramecium* prey individuals at four predator densities two, four, eight, and 16 per 900  $\mu$ l protozoan medium (six replicates at each predator density). The number of encounters with conspecific predators ( $y$ ) was described by the hyperbolic function  $y = \frac{a(P-1)}{1+ab(P-1)}$ , where  $P$  is the predator density, and  $a$  and  $b$  are constants

$i = 2.06 \pm 1.85$  (SE) for the Arditı–Akçakaya and the Beddington–DeAngelis models, respectively (see Table 1).

In the behavioral experiment, the number of encounters with conspecific predators increased as a hyperbolic function of predator density (AIC was larger for both linear and sigmoid functions; Fig. 4). From this model we estimated  $a$  ( $a = 6.94 \pm 3.53$  SE) and  $b$  ( $b = 0.04 \pm 0.01$  SE) on other predators. Although the functional response and the behavioral experiments were conducted under different

conditions (i.e., higher illumination during the behavioral trials), the product of  $a \times b = 0.29$  falls within the SE of the interference parameter ( $i = 2.77 \pm 2.56$  SE) estimated from the Beddington–DeAngelis model.

## Discussion

Recent advances in modeling natural food webs depend on our mechanistic understanding of species interactions. Incorporation of biological realism into simple consumer–resource models can improve our ability to reliably predict complex food web dynamics. Even though the stability effects of functional responses that depend on both predators and prey have been discussed for 40 years, rigorous direct experiments investigating the detailed shape of functional responses over a large gradient of predator and prey densities are still rare.

In our experiments we overcame the limitations of many previous studies and clearly demonstrated predator dependence in the predator's functional response even at low predator densities and after accounting for prey depletion. We detected that the two structurally different models, mechanistic Beddington–DeAngelis and phenomenological Arditı–Akçakaya, surprisingly resulted in closely similar AICc values and parameter estimates (Fig. 3; Table 1). All models with the effect of conspecific predators described our data substantially better than the Holling type III functional response. Analyzing the data with only 1–5 *Stenostomum*/0.9 ml, we confirmed that the functional responses were predator density dependent also at very low predator densities (Figs. 1, 2; Table 1). Quantitative data on natural densities of microturbellaria

are very limited and vary both spatially and seasonally. Natural densities similar to those in our experiment (4 individuals/cm<sup>2</sup>) have been reported from shallow littoral regions (reviewed in Kolasa 2001).

Our results accord with some previous findings from other predator–prey systems. For example, predator-dependent functional responses described 18 of the 19 data sets better than a solely prey-dependent type II functional response (Skalski and Gilliam 2001). Most empirical studies that directly measured predator dependence, however, did not consider the depletion of resources, which might have occurred over the course of the experiments (e.g., Salt 1974; Hayward and Gallup 1976; Helgen 1987; Hansson et al. 2001; Lüring et al. 2003).

Few direct experiments have been conducted on a relatively short time scale to avoid prey depletion, or, alternatively, accounted for prey depletion in their analyses. A prey-dependent type III functional response was demonstrated in a rigorous short-term study of the rotifer *Brachionus calyciflorus* foraging on the green alga *Monoraphidium minutum* (Fussmann et al. 2005). Predator dependence was significant only at unusually high rotifer densities of ~125 *Brachionus*/1 ml (Fussmann et al. 2005). Using the random predator equation, the predation rate of the clerid beetle (*Thanasimus dubius*) feeding on the bark beetle (*Dendroctonus frontalis*) was shown to be strongly dependent on predator density (Reeve 1997). Corroborating prior studies (Schenk et al. 2005; Tschanz et al. 2007), we estimated the interference parameter at an intermediate level between the two extreme models ( $m = 0.67$ ), with the value shifting the equation closer to ratio dependence than to pure prey dependence. Values much closer to the extreme cases for two species of invasive crabs ( $m = 0.9$  for *Carcinus maenas* and  $m = 0.1$  for *Hemigrapsus sanguineus*) were also found (Griffen and Delaney 2007). These authors suggest that the strength of predator dependence can be specific to different predator species. The ratio-dependent model lacks a clear mechanistic basis (Abrams 1994), but functional response models can be viewed on a continuous scale for the degree of predator dependence (Stow et al. 1995). This could be more productive than viewing prey- and predator-dependent models solely as competing alternatives. The magnitude of predator interference estimated from the mechanistic Beddington–DeAngelis model ( $i = 2.77$ ) also suggested that consumption rates were modified by densities of conspecifics.

Furthermore, we obtained some support for the effect of predator density from the behavioral observations. We found that flatworm predators waste a relatively large amount of time during encounters with each other (Fig. 4). Such an increase in the proportion of a predator's time spent on interactions with conspecifics inevitably reduces the time available for other activities including feeding.

Many mechanisms have been suggested to generate predator-dependent functional responses (e.g., Crowley and Martin 1989; Cosner et al. 1999; Crumrine 2005; Rudolf 2006, 2007). Although size-related interference probably plays a minimal role in our model system, we have observed a tendency of *Stenostomum* predators to aggregate spatially with many inter-individual contacts (personal observations from culturing *Stenostomum* and other experiments). Time spent in this common behavior will lead to reduced foraging time. While we have focused on changes in predator behavior, prey are also known to alter their behavior in response to predators. Prey are predicted to reduce their vulnerability when predation risk increases (Werner and Anholt 1993). Consequently, increasing predator density may reduce per capita predation rates through modification of prey behavior (Anholt and Werner 1995). Such anti-predator behavior has been well documented in ciliates (Kusch 1993). Although we only have evidence for direct interference among predators, it is clear that both direct and indirect effects of predator density can simultaneously result in predator dependence in many systems. More empirical work is needed in order to determine the reasons for variation in the degree of predator dependence in functional responses and to identify the underlying mechanisms.

Choosing appropriate functional responses is crucial for adequate predictions of food web dynamics. When predator dependence is incorporated into predator–prey models their stability is usually enhanced (DeAngelis et al. 1975; Arditi et al. 2004; Rall et al. 2008). There is now evidence to show that predation is modulated by the densities of prey (simple functional responses), by the density and diversity of other non-prey species (Vos et al. 2001; Kratina et al. 2007), and by other predators (this study). Such multiple dependencies of functional responses that include prey, non-prey, and predators are essential for a full understanding of food-web dynamics.

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