

## Effects of predator confusion on functional responses

Jonathan M. Jeschke and Ralph Tollrian

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When confronted with a swarm of their prey, many predators become confused and are less successful in their attacks. To shed light on the ecological, ethological and evolutionary consequences of predator confusion, we here investigate its effects on predator functional responses. We develop the first functional response model that considers confusion and compare it (1) qualitatively as well as (2) quantitatively to empirical data from two predator–prey systems, *Aeshna cyanea* (Odonata)–*Daphnia magna* (Crustacea) and *Chaoborus obscuripes* (Diptera)–*Daphnia obtusa*.

(1) The qualitative comparisons show that, contrary to common belief, confusion does not necessarily lead to a dome-shaped functional response. The response can alternatively remain qualitatively unchanged and be affected only quantitatively. A non-dome-shaped response is thus no indication for the absence of predator confusion. The same is true for other swarming effects reducing foraging success, such as early warning of approaching predators. Our results hence question studies that have equated the absence of a dome-shaped response with the absence of a swarming effect. Our results also resolve the apparent paradox that swarming effects are quite common while dome-shaped functional responses are rather uncommon.

(2) There is a good quantitative match between a parameterized version of our model and the empirically measured functional response in the *Chaoborus-Daphnia* system, suggesting that all crucial factors in this system are captured by the model.

*J. M. Jeschke and R. Tollrian, Dept Biologie II, Ludwig-Maximilians-Universität München, Großhaderner Straße 2, DE-82152 Planegg-Martinsried, Germany. Present address for JMJ: Inst. of Ecosystem Studies, P.O. Box AB, Millbrook, NY 12545-0129, USA (jonathan.jeschke@gmx.net). Present address for RT: Dept of Biological Sciences, Lancaster Univ., I.E.N.S., Lancaster, UK, LA1 4YQ.*

Animals often form swarms which provide them with several benefits. For example, they find food faster when they search together, they save energy when they move together, or they have a lower predation risk when they are together. The lower predation risk can be the result of a dilution effect and/or one or more swarming effects that reduce predator foraging success, e.g. early warning of approaching predators, active defence against predators, or confusion of predators. The latter is the focus of this study. This confusion effect is present if predators that are confronted with a swarm of their prey are restricted by their neuronal abilities and are thus less successful in their attacks (Bertram 1978, Krause and Ruxton 2002).

Although confusion is widespread among predators, it has not been incorporated in predator–prey theory, especially functional response models, i.e. models that simulate the number of prey eaten per unit of time (predation rate) as a function of prey density (Solomon 1949). According to their shape, functional responses are usually classified as either type I (predation rate increases linearly with prey density up to a threshold and is constant beyond), type II (the increase is decelerating), or type III (the increase is sigmoid) (Holling 1959a; for a more detailed subdivision of functional response types, see Jeschke et al. 2004). Functional response models form the basis of population dynamics models and foraging theory. They are thus

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important to many ecological, evolutionary and ethological questions. The functional response model we develop here is the first to consider predator confusion. We analyse this model and qualitatively as well as quantitatively compare it to empirical data from two predator-prey systems, *Aeshna cyanea* (Odonata)-*Daphnia magna* (Crustacea) and *Chaoborus obscuripes* (Diptera)-*Daphnia obtusa*.

## Material and methods

### The model

Our model is based on the SSS (steady-state satiation) equation given by Jeschke et al. (2002):

$$y(x) = \begin{cases} \frac{(1 + ax(b + c) - \sqrt{1 + ax(2(b + c) + ax(b - c)^2)})t}{2abcx} & a, b, c, x > 0 \\ \frac{atx}{1 + abx} & b > 0, c = 0 \\ \frac{atx}{1 + acx} & b = 0, c > 0 \\ \frac{atx}{0} & b = c = 0 \\ 0 & a = 0 \text{ or } x = 0 \end{cases} \quad (1)$$

with success rate  $a = \beta\gamma\delta\varepsilon$

and handling time  $b = \frac{t_{att}}{\varepsilon} + t_{eat}$

where  $\beta$  is the encounter rate between a searching predator and a single prey item (dimension in SI units:  $m^2 s^{-1}$  for two-dimensional, e.g. terrestrial, habitats;  $m^3 s^{-1}$  for three-dimensional, e.g. aquatic, habitats);  $\gamma$  is the probability that the predator detects encountered prey (dimensionless);  $\delta$  is the probability that the predator attacks detected prey (dimensionless);  $\varepsilon$  is the efficiency of attack (dimensionless), i.e. the frequency of successful attacks;  $c$  is digestion time per prey item (s);  $t$  is total time (s), i.e. the length of the time interval of interest, e.g. one day or the duration of an experiment;  $t_{att}$  is attacking time per prey item (s);  $t_{eat}$  is eating time per prey item (s);  $x$  is prey density ( $m^{-2}$  or  $m^{-3}$ , respectively); and  $y$  is the number of prey eaten (dimensionless).

The SSS equation is an extension of Holling's (1959b) disc equation. In contrast to the latter, the SSS equation (1) considers predator satiation and (2) divides the predation cycle into the five stages search, encounter, detection, attack, and consumption. (1) It considers satiation by assuming that the searching probability of a predator that is not handling prey depends on its

hunger level. The hunger level, in turn, is assumed to be in a steady-state (cf. "steady-state satiation" equation) determined by consumption rate  $y(x)$  and digestion time  $c$ . (2) The quite detailed subdivision of the predation cycle allows to calculate predator success rate  $a$  on the basis of the parameters encounter rate  $\beta$ , detection probability  $\gamma$ , attacking probability  $\delta$  and attack efficiency  $\varepsilon$ . The SSS equation also considers the time the predator wastes due to unsuccessful attacks: a low attack efficiency  $\varepsilon$  leads to a long handling time  $b$ . See Jeschke et al. (2002) for further information on the SSS equation.

To simulate the functional response of a predator that shows a confusion effect, the constant  $\varepsilon$  in the SSS equation has to be replaced by an attack efficiency  $\varepsilon(x)$  that is free to decrease with increasing prey density  $x$ .

The empirical data summarized by Jeschke and Tollrian (unpubl.) as well as Krakauer's (1995) neural network model suggest that in predators showing a confusion effect, the decrease in attack efficiency with prey density is decelerating and that attack efficiency mostly does not fall below a minimum value which corresponds to complete confusion:

$$\varepsilon(x) = \exp(-\varepsilon_s x) \times (\varepsilon_{max} - \varepsilon_{min}) + \varepsilon_{min} \quad (2)$$

where  $\varepsilon_{max}$  ( $= \varepsilon(0)$ ) is maximum attack efficiency (dimensionless),  $\varepsilon_{min}$  ( $= \lim_{x \rightarrow \infty} \varepsilon(x)$ ) is minimum attack efficiency (dimensionless), and  $\varepsilon_s$  (dimensionless) is a shape parameter that regulates the curve's decrease with increasing prey density  $x$  (Fig. 1). If  $\varepsilon_{min}$  is zero (cf. Cresswell 1994), Eq. 2 simplifies to:  $\varepsilon(x) = \exp(-\varepsilon_s x) \times \varepsilon_{max}$ .

### Empirical functional responses

To empirically investigate how predator confusion affects functional responses, we analyzed the responses

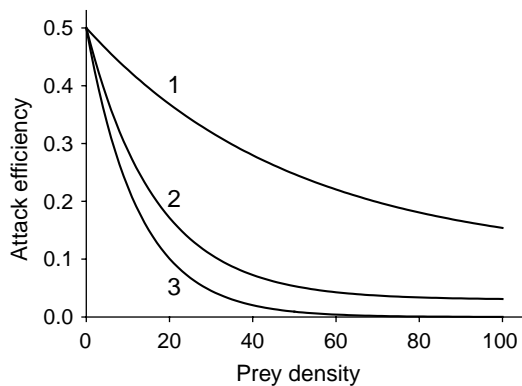


Fig. 1. Graphical representation of Eq. 2. Parameter values for curve 1: maximum attack efficiency  $\epsilon_{\max}=0.5$ , minimum attack efficiency  $\epsilon_{\min}=0.1$ , shape parameter  $\epsilon_s=0.02$ ; parameter values for curve 2:  $\epsilon_{\max}=0.5$ ,  $\epsilon_{\min}=0.03$ ,  $\epsilon_s=0.06$ ; parameter values for curve 3:  $\epsilon_{\max}=0.5$ ,  $\epsilon_{\min}=0$ ,  $\epsilon_s=0.08$ .

of predators that showed a confusion effect in a companion study (J. M. Jeschke and R. Tollrian, unpubl.), *Aeshna cyanea* (Odonata) preying on *Daphnia magna* (Crustacea) and *Chaoborus obscuripes* (Diptera) preying on *Daphnia obtusa*. In either system, confusion was evident due to a decreasing attack efficiency of the predator with increasing prey density. In either predator–prey system, single predators were transferred to defined numbers of *Daphnia* and were in this way confronted with a large range of prey densities, up to those occurring naturally in swarms (Malone and McQueen 1983, Davies 1985, Kvam and Kleiven 1995). This direct confrontation precluded complications arising from the avoidance of swarms by predators (Milinski 1979). To prevent ontogenetic effects, we used predators of the same larval stage at each prey density. We caught the predators in southern Bavarian ponds, while the prey came from laboratory cultures that originated from such ponds. The experiments were performed at room temperature, and the experimental volume varied between the systems in approximate accordance to the size differences between the predator species. All predators were hungry at the beginning of an experiment and experimental time began with the first attack of the predator. The experiments were short to prevent influences from satiation of the predators. Eaten prey were not replaced in order to avoid predator irritation and because the numbers of prey eaten were small compared to the numbers of prey present. In case of *Aeshna cyanea*–*Daphnia magna*, each of seven prey densities was replicated five times except prey density 200 which was replicated four times. The experiments ran with 3rd and 4th juvenile instar *D. magna* in a volume of 280 ml (diameter = 11 cm, water depth = 3 cm) and lasted 2 min. In case of *Chaoborus obscuripes*–*Daphnia obtusa*, we used 4th instar larvae (mean length = 12 mm) and ten replicates for each of eight prey densities. To standardize

the *Daphnia* to an equal size, they were sieved; used were those that passed a 500  $\mu\text{m}$  gauze but were retained by a 200  $\mu\text{m}$  one. Here, the experimental volume was 40 ml (diameter = 5 cm, water depth = 2 cm) and the duration 30 min.

In either predator–prey system, we statistically analyzed the data as follows: we fitted a logistic regression model to the number of prey eaten vs prey density (Trexler et al. 1988, Hosmer and Lemeshow 1989, Juliano 1993, Sokal and Rohlf 1995, Jeschke and Tollrian 2000). Furthermore, in order to check whether the number of prey eaten decreased at high prey densities (i.e. broad sense dome-shaped response, otherwise type II response), we compared the mean number of prey eaten at high densities to that at intermediate ones via t-tests (for unequal variances if necessary).

## Evaluation of the model

To allow for a quantitative evaluation of our model, it must be adapted to the experimental conditions. Two main assumptions underlying our model are that prey density and predator hunger level are constant (Jeschke et al. 2002). These assumptions are more or less valid in the field but are usually violated in laboratory experiments, including the ones analyzed here, where eaten prey are normally not replaced and the predators are often pre-starved. Therefore, by allowing prey density to decrease and the hunger level to vary, we extend the steady-state satiation (SSS) equation (Eq. 1) to the satiation model (Eq. A1, A2, A3; Appendix A). We combine the satiation model with Eq. 2, which simulates predator confusion, parameterize it with data from the *Chaoborus*–*Daphnia* system (Appendix B), and compare the resulting simulated functional response to the empirically measured response. We have not done this for the *Aeshna*–*Daphnia* system as well because of a lack of data for the model parameterization.

## Results

### Theoretical results

The analysis of the extended SSS equation (combination of Eq. 1, 2) revealed that predator confusion can affect a functional response in three different ways (Fig. 2). First, the response can become dome-shaped in the narrow sense, i.e. at high prey densities, prey uptake decreases towards zero. Second, the response can become “roller-coaster-shaped” (this is a new type of functional response), i.e. at high prey densities, prey uptake decreases but stops decreasing before it becomes zero and rises again to reach a plateau. These two response types may be summarized as dome-shaped in the broad sense, i.e. prey uptake decreases at high prey

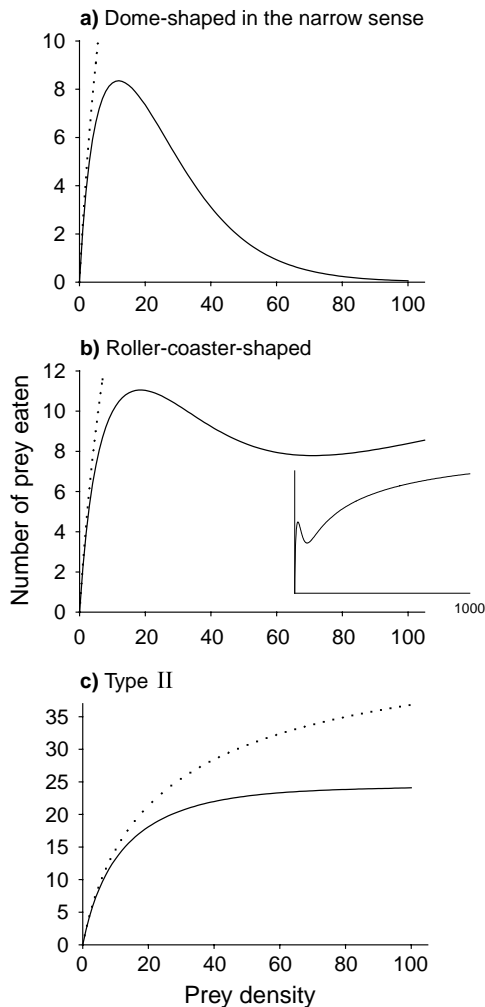


Fig. 2. How predator confusion affects the functional response, theoretical results part I. Solid lines refer to functional responses including confusion; dotted lines correspond to responses without confusion (these are all of type II). The underlying model is the extended SSS equation (Eq. 1, 2), the parameter values were encounter rate  $\beta=10$ , detection probability  $\gamma=0.5$ , attack probability  $\delta=1$ , digestion time  $c=0.02$ , total time  $t=1$ , attacking time  $t_{att}=0.001$ , and eating time  $t_{eat}=0.01$ . (a) Type II becomes dome-shaped in the narrow sense; parameter values are equal to curve 3 in Fig. 1: maximum attack efficiency  $\epsilon_{max}=0.5$ , minimum attack efficiency  $\epsilon_{min}=0$ , shape parameter  $\epsilon_s=0.08$ . (b) Type II becomes roller-coaster-shaped; parameter values are equal to curve 2 in Fig. 1:  $\epsilon_{max}=0.5$ ,  $\epsilon_{min}=0.03$ ,  $\epsilon_s=0.06$ . The plateau of a roller-coaster-shaped response (insert) lies for most species probably beyond the range of naturally occurring prey densities. (c) Type II remains type II but the plateau is lowered and is reached earlier; parameter values are equal to curve 1 in Fig. 1:  $\epsilon_{max}=0.5$ ,  $\epsilon_{min}=0.1$ ,  $\epsilon_s=0.02$ .

densities. Third, the functional response can remain qualitatively unchanged and is affected only quantitatively: type II remains type II but the plateau is lowered and is reached earlier. The conditions leading to each of these three types of functional response are outlined in Fig. 3.

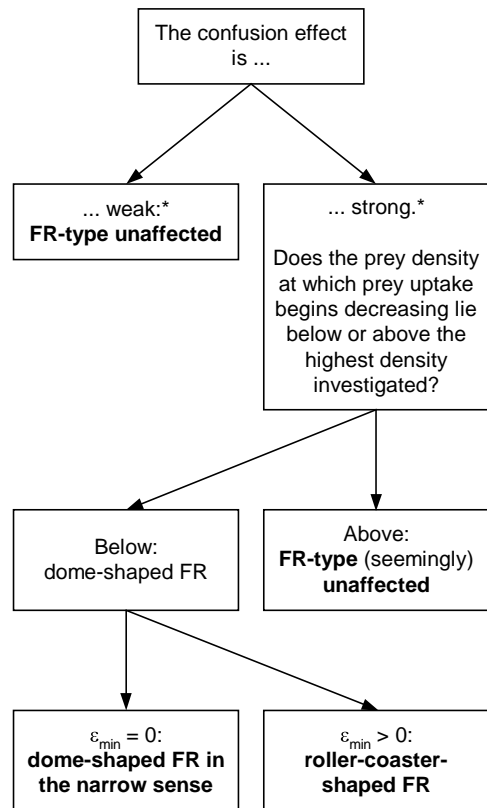


Fig. 3. How predator confusion affects the functional response, theoretical results part II. Note: \*A confusion effect is called “strong” here if either minimum attack efficiency  $\epsilon_{min}=0$  or the ratio of maximum to minimum attack efficiency,  $\epsilon_{max}/\epsilon_{min}$ , is high. For  $\epsilon_{min}>0$ , we mathematically define a weak or strong confusion effect due to the complexity of our model only for the simplified case handling time  $b=0$ . If  $\epsilon_{min}>0$  and  $b=0$ , the functional response remains type II, i.e. the confusion effect is weak, if  $\epsilon_{max}/\epsilon_{min} \leq \exp(2)+1 \Leftrightarrow \epsilon_{max}/\epsilon_{min} \leq 8.39$ . Otherwise the response becomes roller-coaster-shaped, i.e. the confusion effect is strong. The derivation of this inequality is available from JMJ upon request.

## Empirical results

The functional responses of *Aeshna cyanea* preying on *Daphnia magna* and of *Chaoborus obscuripes* preying on *Daphnia obtusa* are shown in Fig. 4. Larval *Aeshna cyanea* showed a roller-coaster-shaped response: at high prey densities, prey uptake decreased (the difference in the number of prey eaten between intermediate prey densities (50, 100, 150) and high prey densities (200 and 250) is significant ( $P<0.01$ , one-tailed t-test)) but the decrease stopped before prey uptake became zero (the logistic regression model parameter for the squared prey density is significantly larger than zero ( $P<0.01$ , one-tailed Wald test)). The maximum number of prey eaten in 2 min was 8.6 (at prey density 100). The functional response of *Chaoborus obscuripes* preying on *Daphnia obtusa* may be classified as type II because the predation

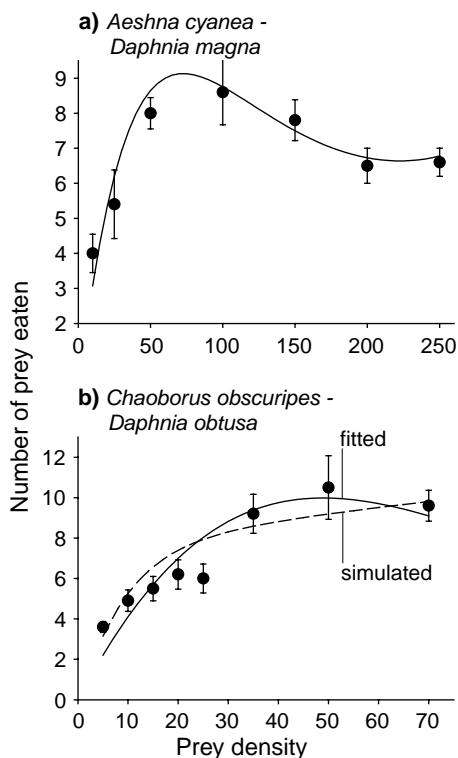


Fig. 4. How predator confusion affects the functional response, empirical results; circles are means  $\pm$  SE, solid lines are logistic regression fits. (a) *Aeshna cyanea*–*Daphnia magna*: roller-coaster shaped functional response,  $T=2$  min,  $V=280$  ml, logistic regression fit:  $y = [\exp(-0.60272 - 0.02151x + 0.000038x^2) x] / [1 + \exp(-0.60272 - 0.02151x + 0.000038x^2)]$ . (b) *Chaoborus obscuripes*–*Daphnia obtusa*: type II functional response,  $T=30$  min,  $V=40$  ml, logistic regression fit ( $r=0.624$ ):  $y = [\exp(-0.10634 - 0.02565x)x] / [1 + \exp(-0.10634 - 0.02565x)]$ , dashed line: parameterized satiation model (correlation between simulated and observed values:  $r=0.612$ ; Eq. A1, A2, A3, 2; parameter values are given in Appendix B).

rates that were observed at the two highest prey densities do not significantly differ ( $P=0.308$ , one-tailed t-test for unequal variances). The maximum number of prey eaten in 30 min was 10.5 (at prey density 50).

### Evaluation of the model

As shown in Fig. 4b, the functional response of *Chaoborus obscuripes* preying on *Daphnia obtusa* simulated by our model agrees well with the observed one:  $r=0.612$  ( $P<0.001$ , two-tailed). These values are similar to those of a logistic regression fit of the empirical data:  $r=0.624$  ( $P<0.001$ , two-tailed). Our model is insensitive to changes in *Daphnia* body length: using 0.8 mm for *Daphnia* body length instead of 0.7 mm results in  $r=0.610$  (instead of 0.612).

### Discussion

This study extended the SSS equation to the first functional response model that includes predator confusion (Jeschke et al. 2002). As shown above, there is a good agreement between the extended SSS equation presented here and empirical data from laboratory experiments in the *Chaoborus*–*Daphnia* system, and this is probably not the only system where the consideration of success rate, handling time, digestion time, and swarming effects reducing predator foraging success is sufficient to adequately predict a laboratory functional response. We are less optimistic for field functional responses where learning, switching, and adaptive behaviour may often be relevant as well, depending on the focal predator–prey system.

According to conventional wisdom, confusion and other swarming effects that reduce foraging success let functional responses become dome-shaped (Young et al. 1994, Watt and Chapman 1998). We have both theoretically and empirically shown that they can also remain qualitatively unaffected. Because we performed our experiments in small volumes in the laboratory, it is not granted that the two investigated predators show the same functional responses in the field. On the other hand, Jeschke et al.'s (2004) review of empirical functional responses revealed that the distribution of different types of functional response does not differ between the laboratory and the field. Considering the available evidence, we can reasonably conclude that swarming effects do in general not necessarily lead to dome-shaped responses. The relevance of this finding will be highlighted by three examples.

#### (1) Functional responses as indicators

According to our finding, a non-dome-shaped response indicates neither the presence nor absence of swarming effects that reduce foraging success. On the other hand, a dome-shaped response in the broad sense indicates that at high prey densities, the predator either shows such a swarming effect or avoids unpalatable prey due to learning (Holling 1965, Heinrich and Vogt 1980, Brönmark et al. 1984).

#### (2) How common are swarming effects that reduce foraging success?

Swarming effects that reduce foraging success must be more common than dome-shaped responses in the broad sense. This finding resolves the apparent paradox that dome-shaped responses are less common than swarming effects: Jeschke et al. (2004) reviewed more than 800 functional responses and found about 10% to be dome-shaped. On the other hand, we found that in 64% of the 25 predator–prey systems studied to date, the predators became confused (unpubl.).

### (3) Fitting functional responses

Type II responses have mostly been fitted with either the disc equation (Holling 1959b), the random predator equation (Royama 1971, Rogers 1972), or the Gause-Ivlev equation (Gause 1934, Ivlev 1961). Regression equations obtained in this way include one parameter that represents the maximum number of prey eaten. For example, in the disc and the random predator equation, the parameter “handling time”  $t_h$  is the reciprocal value of the maximum number of prey eaten. Our results demonstrate that the term “handling time” is misleading: real handling time and the parameter  $t_h$  have little in common (Fox and Murdoch 1978, Abrams 1990, Caldow and Furness 2001, Jeschke et al. 2002). This is because the maximum number of prey eaten is naturally determined by many factors including handling time, digestion time, learning, switching, adaptive behaviour, and – as shown here – swarming effects that reduce foraging success. These factors are amalgamated by the parameter  $t_h$  in an unknown way. Therefore, the value of the parameter  $t_h$  obtained by fitting an empirical functional response cannot be biologically interpreted.

If a swarming effect reducing foraging success does qualitatively affect the functional response of a predator, it leads to a dome-shaped curve which can be either dome-shaped in the narrow sense or roller-coaster-shaped. A narrow sense dome-shaped curve reaches zero at very high prey densities, whereas a roller-coaster-shaped curve decreases at high prey densities but stops decreasing before it becomes zero and rises again to reach a plateau (Fig. 2). For most species, however, this plateau probably lies beyond naturally occurring prey densities. A functional response is roller-coaster-shaped rather than dome-shaped in the narrow sense if the predator's foraging success is positive even at the highest prey densities. It is dome-shaped in the narrow sense if foraging success drops to zero at high prey densities (Fig. 3; in case of the confusion effect, the relevant foraging success parameter is attack efficiency  $\varepsilon$ ).

The functional response model developed here can be easily further extended, e.g. to two types of prey or to different prey to predator size ratios (empirically addressed by Hirvonen and Ranta 1996). The basic or extended model may also serve as a basis for predator-prey population models or adaptive behaviour models that include predator confusion, e.g. models that simulate predators foraging in a patchy environment where each patch consists of one prey swarm. Since predator confusion is similar to other swarming effects that reduce predator foraging success, such models may not only reveal ecological, evolutionary, and ethological consequences of predator confusion but of defence functions of gregariousness in general.

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## Appendix A. The satiation model

Here we extend the steady-state satiation (SSS) equation (Eq. 1) to the satiation model. For this extension, we refer to the functional response model that underlies the SSS equation (Jeschke et al. 2002):

$$\frac{dy(t)}{dt} = \frac{h(t)ax(t)}{1 + h(t)abx(t)} \quad (\text{A1})$$

for success rate  $a$  and handling time  $b$ , see Eq. 1. The number of prey eaten  $y(t)$  is obtained by integration. In the satiation model, prey density has an initial value  $x(0)$  and is decreased by predation:

$$x(t) = x(0) - y(t) \quad (\text{A2})$$

Furthermore, predator hunger level  $h(t)$  is allowed to vary. Hunger level is the proportion of empty volume of that part of the gut that is responsible for feelings of hunger and satiation. For most predator species, this is the stomach or the crop;  $h=0$  means no hunger, i.e. full gut, and  $h=1$  means 100% hunger, i.e. empty gut. The hunger level has an initial value  $h(0)$ , is increased by digestion and decreased by ingestion. For extreme

parameter values, it is necessary to define the process of digestion for hunger levels beyond the interval  $[0; 1]$ . Therefore,

$$\frac{dh(t)}{dt} = \begin{cases} \frac{1}{t_g} - s \frac{dy(t)}{dt} & h(t) < 0 \\ \frac{1 - h(t)}{t_g} - s \frac{dy(t)}{dt} & 0 \leq h(t) \leq 1 \\ -s \frac{dy(t)}{dt} & h(t) > 1 \end{cases} \quad (\text{A3})$$

where  $s$  is the satiation per prey item, i.e. the reciprocal capacity of the hunger-determining part of the gut; for example, if a man is satiated with 10 potatoes in his stomach, then  $s=0.1$ ; and  $t_g$  is gut retention time which equals the parameter  $t_{\text{dig}}$  in Jeschke et al. (2002). A negative value for  $h$  means that the predator caught a prey item too large to eat whole. The predator will feed to satiation and store the rest until being hungry again. When the whole prey item is gone,  $h$  will again be positive. On the other hand, a value of  $h$  larger than 1 means that the predator is starving. The complete satiation model consists of the coupled Eq. A1, A2 and A3.

**Appendix B. The extended satiation model (Eq. A1, A2, A3, 2) parameter values for our experiments in the *Chaoborus–Daphnia* system**

Parameter	Value	Source
<i>Daphnia</i> density X (related to an experimental volume of 40 ml)	5, 10, 15, 20, 25, 35, 50, 70	this study
Encounter rate $\beta$ (related to an experimental volume of 40 ml)	0.21 min <sup>-1</sup>	Giguère et al. (1982), Dodson and Ramcharan (1991) <sup>1</sup>
Product of detection probability $\gamma$ and attack probability $\delta$	0.46	Giguère et al. (1982)
Maximum attack efficiency $\varepsilon_{\max}$	0.48	Jeschke and Tollrian (unpubl.) <sup>2</sup>
Minimum attack efficiency $\varepsilon_{\min}$	0.12	Jeschke and Tollrian (unpubl.) <sup>2</sup>
Shape parameter $\varepsilon_s$	0.051	Jeschke and Tollrian (unpubl.) <sup>2</sup>
Initial hunger level h(0)	1	Jeschke and Tollrian (unpubl.)
Satiation per <i>Daphnia</i>	0.095	this study <sup>3</sup>
<i>Chaoborus</i> handling time b	0.023 min	Pastorok (1981) <sup>4</sup>
<i>Chaoborus</i> gut retention time t <sub>g</sub>	447 min	Giguère (1986) <sup>5</sup>
Duration of an experiment	30 min	Jeschke and Tollrian (unpubl.)

Notes:

$$(1) \beta = v \times \pi \times \frac{R' \times L_t}{2 \times V} \quad (\text{A4; Giguère et al. 1982})$$

where  $v$  is *Daphnia* swimming velocity,  $R'$  is *Chaoborus* encounter field radius,  $L_t$  is *Chaoborus* encounter field length, and  $V$  is experimental volume. *Daphnia* swimming velocity  $v$  has been calculated as

$$v = 2.444 \text{ mm s}^{-1} + \textit{Daphnia length (mm)} \times 0.853 \times \text{s}^{-1}. \quad (\text{A5})$$

We have obtained Eq. A5 by linearly regressing ( $r = 0.844$ ) empirical data given by Dodson and Ramcharan (1991).

*Chaoborus* encounter field radius  $R'$  has been computed as

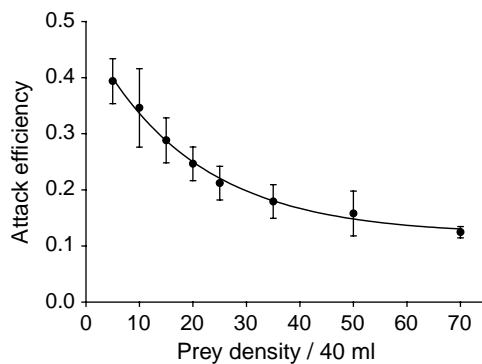
$$R' = \textit{Chaoborus length} \times (2.2/14.8) + \textit{Daphnia length}/(1.75 \times 2). \quad (\text{A6; Giguère et al. 1982})$$

Finally, *Chaoborus* encounter field length  $L_t$  has been calculated as

$$L_t = \textit{Chaoborus length} + 2 R'. \quad (\text{A7; Giguère et al. 1982})$$

Here, experimental volume  $V = 40 \text{ ml} = 40 \times 10^3 \text{ mm}^3$ , *Chaoborus* length = 11.59 mm, and *Daphnia* length  $\approx 0.7 \text{ mm}$ , giving  $v = 3.04 \text{ mm/s}$ ,  $R' = 1.92 \text{ mm}$ , and  $L_t = 15.44 \text{ mm}$ . Inserting these values into Eq. A4 yields encounter rate  $\beta = 0.0035 \text{ s}^{-1} = 0.21 \text{ min}^{-1}$ . Note that Giguère et al. (1982) gave encounter rate relative to the experimental volume, i.e. without a spatial dimension. To account for this, food abundance  $x$  is also given without a spatial dimension here.

2) The values for the maximum attack efficiency  $\varepsilon_{\max}$ , the minimum attack efficiency  $\varepsilon_{\min}$ , and the shape parameter  $\varepsilon_s$  have been obtained by a non-linear regression fit of Eq. (2) to the empirical data given by Jeschke and Tollrian (unpubl.): attack efficiency  $\varepsilon(x) = \exp(-0.051x) \times (0.48 - 0.12) + 0.12$  ( $r = 0.619$ ). In the following graph, this regression line is plotted together with the empirical data (means  $\pm$  SE):



(3) The given value is the reciprocal observed maximum number of prey eaten (= 10.5). This estimation is possible because no complete digestion took place during our short-term experiments.

$$(4) b = 0.0203 \times \exp(\textit{Daphnia length} \times 2.74)/60 \quad (\text{A8; Pastorok 1981})$$



$$(5) t_g = (5.538 + 4.140 \times Daphnia \text{ length (mm)}^{2.17}) \times 60 \quad (\text{A9})$$

We have obtained Eq. A9 by linearly regressing ( $r=0.925$ ) empirical data given by Giguère (1986),

$$t_g = (5.538 + 696.903 \times Daphnia \text{ mass } (\mu\text{g})) \times 60, \quad (\text{A10})$$

and by replacing *Daphnia* body mass with body length (reviewed by Giguère 1986),

$$Daphnia \text{ mass } (\mu\text{g}) = 0.00594 \times Daphnia \text{ length (mm)}^{2.17}. \quad (\text{A11})$$