

# Density-dependent effects of prey defenses and predator offenses

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## Abstract

Defenses protect prey, while offenses arm predators. Some defenses and offenses are constitutive (e.g. tortoise shells), while others are phenotypically plastic and not always expressed (e.g. neckteeth in water fleas). All of them are costly and only adaptive at certain prey densities. Here, I analyse such density-dependent effects, applying a functional response model to categorize defenses and offenses and qualitatively predict at which prey densities each category should evolve (if it is constitutive) or be expressed (if it is phenotypically plastic). The categories refer to the step of the predation cycle that a defense or offense affects: (1) search, (2) encounter, (3) detection, (4) attack, or (5) meal. For example, prey warning signals such as red coloration prevent predator attacks and are hence step 4 defenses, while sharp predator eyes enhance detection and are step 3 offenses. My theoretical analyses predict that step 1 defenses, which prevent predators from searching for their next meal (e.g. toxic substances), evolve or are expressed at intermediate prey densities. Other defenses, however, should be most beneficial at low prey densities. Regarding predators, step 1 offenses (e.g. immunity against prey toxins) are predicted to evolve or be expressed at high prey densities, other offenses at intermediate densities. I provide evidence from the literature that supports these predictions.

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## 1. Introduction

Most prey form defenses against their predators (the terms predator and prey are used in a broad sense here, i.e. predators include carnivores, herbivores, parasites/parasitoids; and prey include all living beings that are partly or totally consumed by predators). Prey defenses reduce predation risk (number of prey consumed divided by prey density), but this protective advantage depends on prey density. For example, Jeschke and Tollrian (2000) reported for an aquatic predator–prey system that body armor is

especially beneficial at low prey densities. An opposite density-dependent effect was found for a defense that increases predator digestion time: it was more beneficial at high prey densities. In the current study, I provide a theoretical basis for these empirical results. I also look at the density-dependent effects of the predators' counterparts to prey defenses, i.e. predator offenses.

My considerations are based on the steady-state satiation (SSS) equation, a functional response model developed by Jeschke et al. (2002; see also Jeschke et al., 2004; Jeschke and Tollrian, 2005). The SSS equation is an extension of Holling's (1959) disc equation and describes a type II functional response (for a review of functional response types, see Jeschke et al., 2004). In contrast to the disc equation, the SSS equation considers predator satiation and partitions the predation cycle into five steps: search,

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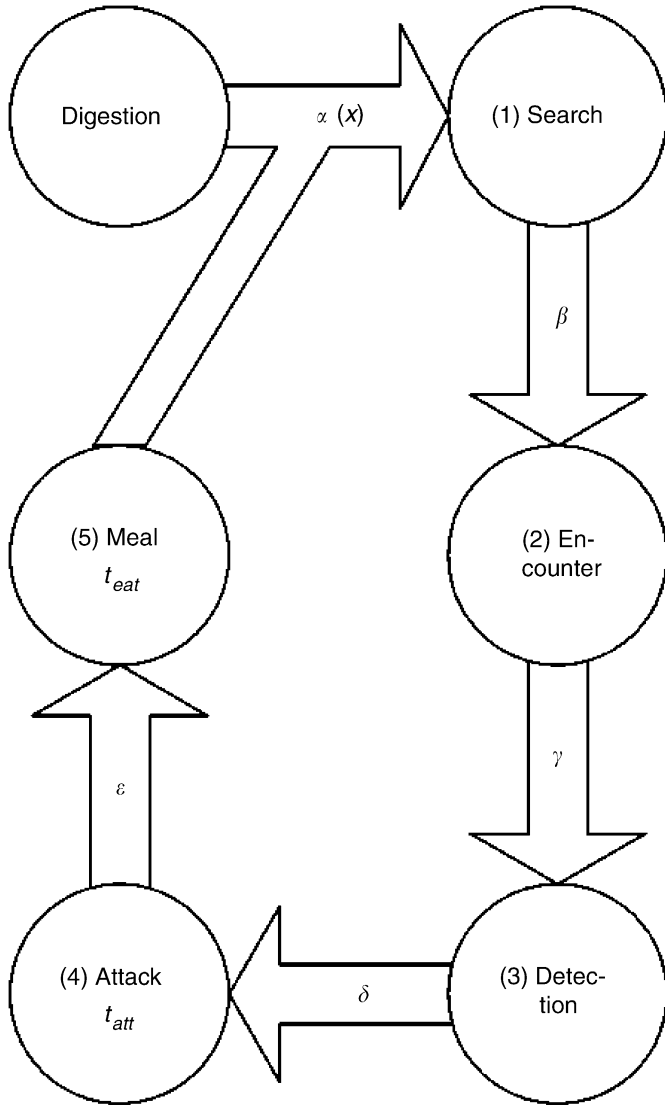


Fig. 1. The predation cycle (modified from Jeschke et al., 2002); parameters are explained in the main text below Eq. (1).

encounter, detection, attack, and meal (Fig. 1). The SSS equation is given by

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

with success rate  $a = \beta \cdot \gamma \cdot \delta \cdot \epsilon$ , handling time  $b = t_{att}/\epsilon + t_{eat}$ , digestion time  $c = t_g/g$ ,

where  $y(x)$  is the predator consumption rate;  $\beta$  the encounter rate between a searching predator and a prey individual (dimension in SI units:  $m^2 s^{-1}$  for a two-dimensional system, e.g. a terrestrial system, and  $m^3 s^{-1}$  for a three-dimensional system, e.g. an aquatic system);  $\gamma$  is the probability that the predator detects encountered prey (dimensionless);  $\delta$  is the probability that the predator attacks detected prey (dimensionless);  $\epsilon$  is attack efficiency (dimensionless), i.e. the probability that an attack is successful;  $t_{att}$  is attacking time per prey individual (s);  $t_{eat}$  is eating time per prey individual (s);  $t_g$  is gut retention time (s); and  $g$  is gut capacity (dimensionless), i.e. the number of prey items the gut of a satiated animal holds.

In the SSS equation, the density dependence of predator consumption rate results from two different processes. First, with increasing prey density, the predator spends more time handling food and has less time available for searching (cf. Holling, 1959). Second, the predator digests larger amounts of food at higher prey densities, reducing its hunger level and its searching effort  $\alpha$ . Searching effort  $\alpha$  is defined as the product of searching probability (how likely it is that the predator, if it is not handling food, searches for food) and searching intensity (scaled from 0 to 1, where the latter represents highest searching intensity, e.g. maximum filtration rate in case of filter feeders, cf. Jeschke et al., 2004). For predators that do not vary the intensity of searching (this is approximately true for cruising carnivores), searching effort equals searching probability. The SSS equation assumes that at each prey density, the predator hunger level reaches a steady state (cf. SSS equation), which equals  $1 - c \times y(x)$ . In summary, searching probability  $\times$  searching intensity =  $\alpha(x) = h(x) = 1 - c \times y(x)$ .

The processes of handling and digesting are assumed to be overlapping rather than mutually exclusive, and the predator's asymptotic maximum consumption rate  $y_{max}$  (for  $x \rightarrow \infty$ ) is limited by the larger of the two terms handling time  $b$  and digestion time  $c$ :  $y_{max}$  is  $1/b$  if  $b \geq c$  (handling-limited predators), and it is  $1/c$  if  $c > b$  (digestion-limited predators). According to Jeschke et al. (2002), most predators are digestion limited. The detailed subdivision of the predation cycle in the SSS equation makes it possible to

$$\begin{aligned} & a, b, c, x > 0, \\ & b > 0, c = 0, \\ & b = 0, c > 0, \\ & b = c = 0, \\ & a = 0 \text{ or } x = 0, \end{aligned} \tag{1}$$

consider the time a predator wastes due to unsuccessful attacks and to classify prey defenses as well as predator offenses according to the step of the predation cycle they

affect. I do this below and qualitatively predict density-dependent effects of each type of defense and offense. I then compare these predictions to empirical data from the literature and show how they can, in turn, be used to predict at which prey densities the benefits of defenses and offenses outweigh their costs. I conclude with a comparison of these predictions to empirical data and with suggestions for future studies.

## 2. Classifying prey defenses

I classify prey defenses into five different types; each type interrupts the predation cycle at a particular step: (1) search, (2) encounter, (3) detection, (4) attack, and (5) meal (Fig. 1).

*Step 1 defenses:* prevent search. (A) Hardly digestible or toxic substances increase predator digestion time  $c$  and thus reduce a predator's motivation to search for the next meal, i.e. they reduce  $\alpha$ . (B) Similarly, prey armor increases predator handling time and thus the time period between two consecutive meals. Note that step 1 defenses do not provide a direct benefit for prey that are already dead when the predator ingests them. They can provide benefit, however, for clonal prey and especially for modular organisms such as plants, fungi, or corals that are still alive when a predator has ingested some modules.

*Step 2 defenses:* prevent encounter. Predator avoidance strategies such as hiding in refuges, diel vertical migration, or slow movements lower the encounter rate  $\beta$  with a predator (Edmunds, 1974; Endler, 1991).

*Step 3 defenses:* prevent detection. Camouflage or freezing reduce a predator's detection probability  $\gamma$  (Edmunds, 1974; Endler, 1991; Ruxton et al., 2004; Caro, 2005).

*Step 4 defenses:* prevent attack. Warning signals such as black-and-yellow coloration in bees or rattling in rattlesnakes decrease the probability  $\delta$  that a predator attacks (Edmunds, 1974; Endler, 1991; Ruxton et al., 2004; Caro, 2005).

*Step 5 defenses:* prevent meal. Armor or flight behavior reduce a predator's attack efficiency  $\varepsilon$  (Edmunds, 1974; Endler, 1991; Ruxton et al., 2004; Caro, 2005). Many step 5 defenses are also step 1B defenses.

This categorization of prey defenses has three advantages over comparable previously proposed classifications. First, it includes step 1 defenses that are usually ignored in such classifications, e.g. in that proposed by Ruxton et al. (2004) or the pre-/post-contact classification where step 2–4 defenses are pooled as pre-contact defenses and step 5 defenses are called post-contact defenses; pre- and post-contact defenses have also been termed primary and secondary defenses, respectively (Edmunds 1974, Swift 1992). Endler's (1991) "consumption defenses" are similar to the step 1 defenses presented here, however. Another advantage of the categorization offered here is its embedding in a theoretical framework, allowing its straightforward application in theoretical analyses. An example for

such an application is given below, where I analyse the benefits of each type of defense depending on prey density. The third advantage of the present classification is that it can easily be extended to predator offenses (see next section). A difficulty with the present categorization is that some defenses (and offenses) fall into more than one category, e.g. armor or flight behavior. As has been noted by Caro (2005), some other classifications of prey defenses have the same difficulty, but it should be kept in mind when applying any of these classifications.

## 3. Classifying predator offenses

As with prey defenses, predator offenses can also be classified according to the step of the predation cycle they affect: (1) search, (2) encounter, (3) detection, (4) attack, and (5) meal. To my knowledge, no comparable categorizations of predator offenses exist.

*Step 1 offenses:* enhance search. (A) Decrease digestion time  $c$ : increase gut capacity  $g$  or decrease gut retention time  $t_g$ . Included herein is immunity against prey toxins. (B) Decrease handling time  $b$ : decrease attacking time  $t_{att}$  or eating time  $t_{eat}$ , or increase attack efficiency  $\varepsilon$ . For example, a higher acceleration when attacking prey decreases attacking time  $t_{att}$  and simultaneously increases attack efficiency  $\varepsilon$ . Step 1 offenses increase searching effort  $\alpha$ .

*Step 2 offenses:* enhance encounter. Increase searching speed or encounter area or volume in which prey are potentially detected (e.g. sharper eyes) or caught (e.g. a larger spider web). These offenses increase the encounter rate  $\beta$  with prey.

*Step 3 offenses:* enhance detection. More responsive senses, e.g. sharper eyes, lead to a higher probability of detection  $\gamma$ . Many step 3 offenses are also step 2 offenses.

*Step 4 offenses:* enhance attack. Immunity against prey toxins (which is also a step 1 offense) or a generally low vulnerability allows the attack of even well defended prey and thus increases the probability of attack  $\delta$ .

*Step 5 offenses:* enhance attack efficiency  $\varepsilon$  by, for example, a higher acceleration during attacks, which is also a step 1 offense.

## 4. Results

Using the SSS equation, I simulated the density-dependent effects of prey defenses and predator offenses (Figs. 2 and 3). The various types of defense and offense differ in their effects on the composite parameters: success rate  $a$ , handling time  $b$ , and digestion time  $c$ . Step 1 defenses and offenses affect handling time  $b$  or digestion time  $c$ . Step 2, 3, and 4 defenses are qualitatively identical because their only effect is to reduce predator success rate  $a$ . Similarly, step 2, 3, and 4 offenses all increase and only increase  $a$ . In Figs. 2 and 3, they are therefore shown together. The density-dependent effects of step 5 defenses or offenses are similar to step 2, 3, and 4 defenses or

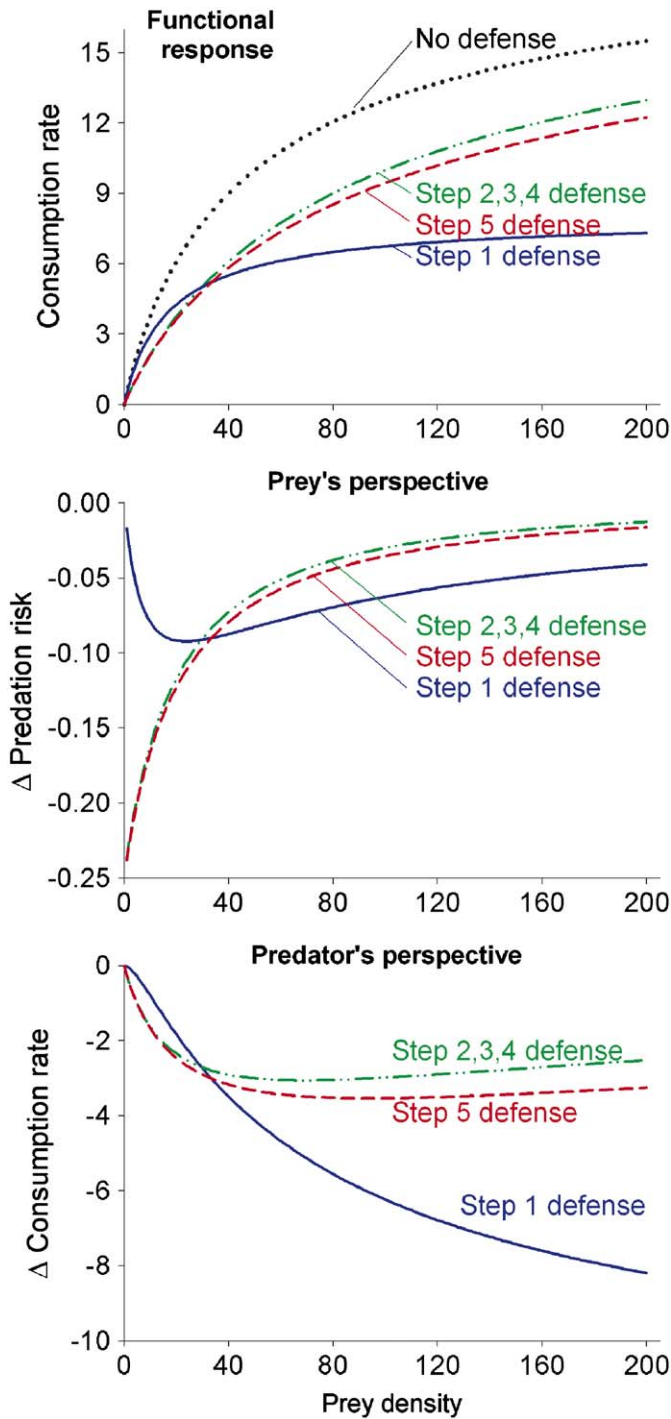


Fig. 2. Density-dependent effects of prey defenses.  $\Delta$  Predation risk is the predation risk of defended prey minus that of undefended prey. Analogously,  $\Delta$  consumption rate is the consumption rate for defended prey minus that of undefended prey. Model inputs (SSS equation, Eq. (1): no defense (dotted line):  $\beta = 2$ ,  $\gamma = 0.5$ ,  $\delta = 1$ ,  $\epsilon = 0.5$ ,  $t_{att} = 0.005$ ,  $t_{eat} = 0.01$ ,  $t_g = 0.1$ ,  $g = 2$ . Step 1 defense (solid line):  $t_g = 0.25$ , otherwise as “no defense”. Step 2, 3, 4 defense (dash-dotted line):  $\gamma = 0.25$ , otherwise as “no defense”. Step 5 defense:  $\epsilon = 0.25$ , otherwise as “no defense”.

offenses, respectively. However, they do not only affect predator success rate  $a$ , but also handling time  $b$ .

Step 1 defenses decrease prey predation risk especially at intermediate prey densities. At low densities, they are not

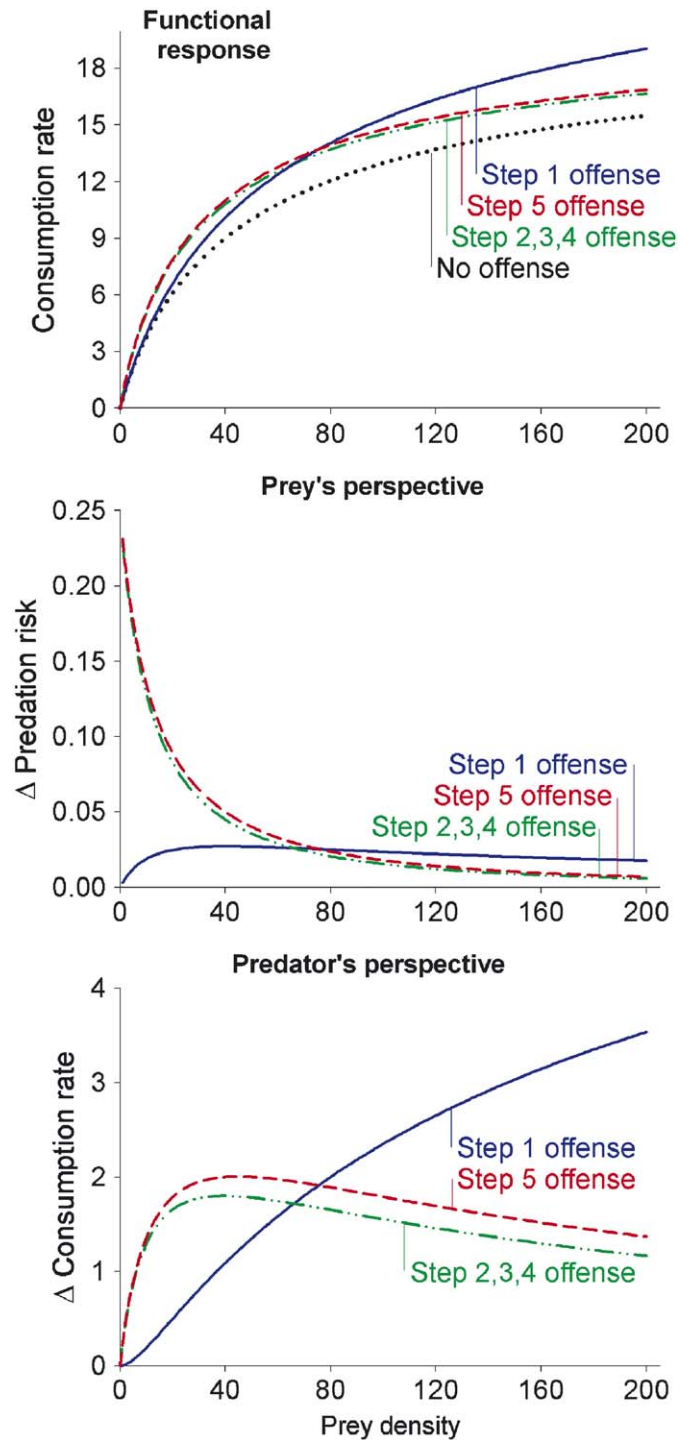


Fig. 3. Density-dependent effects of predator offenses.  $\Delta$  Predation risk is the predation risk for predators with an offense minus that for predators without the offense. Analogously,  $\Delta$  consumption rate is the consumption rate of predators with an offense minus that of predators without the offense. Model inputs (SSS equation, Eq. (1): no offense (dotted line):  $\beta = 2$ ,  $\gamma = 0.5$ ,  $\delta = 1$ ,  $\epsilon = 0.5$ ,  $t_{att} = 0.005$ ,  $t_{eat} = 0.01$ ,  $t_g = 0.1$ ,  $g = 2$ . Step 1 offense (solid line):  $g = 2.75$ , otherwise as “no offense”. Step 2, 3, 4 offense (dash-dotted line):  $\gamma = 0.75$ , otherwise as “no offense”. Step 5 defense:  $\epsilon = 0.75$ , otherwise as “no offense”.

effective because the predator is neither handling nor digestion limited. At high densities, safety-in-numbers—which has also been termed the dilution effect (Hamilton,

1971; Treisman, 1975; Foster and Treherne, 1981)—overrides the effect of the defense. In other words, the predator's consumption rate is limited by its handling or digestion time even if prey are undefended. The safety-in-numbers effect operates for all types of defense and offense. Step 1 defenses decrease predator consumption rate especially at high prey densities.

Step 2, 3, 4 defenses are most beneficial at low prey densities because safety-in-numbers diminishes the defense effect with increasing prey densities. Step 2, 3, 4 defenses decrease absolute predator consumption rate especially at intermediate prey densities. At low densities, the effect is small in absolute numbers but high in relation to the low consumption rates achieved by predators at these densities. From an intermediate to high prey density, the defense effect on consumption rate decreases with prey density because consumption rate becomes more dependent on handling or digestion time, which are not influenced by step 2, 3, 4 defenses.

Step 5 defenses affect prey predation risk and predator consumption rate in the same way as step 2, 3, 4 defenses if the predator is digestion limited. For handling-limited predators, the density dependence of the protective advantage remains qualitatively the same as well but the decrease in predator consumption rate is highest at high densities. Since handling-limited predators are rare (Jeschke et al., 2002), the corresponding simulations are not shown.

The density dependence of the effect of each type of predator offense is analogous to the corresponding type of prey defense, but the direction of the effect is, of course, reversed (Fig. 3). For example, the effect of step 1 offenses and step 1 defenses on predation risk is maximal at intermediate prey densities, but the offense leads to an increase in predation risk whereas the defense leads to a decrease.

## 5. Discussion

### 5.1. Comparison to empirical data

I now compare the simulation results to empirical data from Jeschke and Tollrian (2000) and Esaias and Curl (1972) (Fig. 4). Surprisingly, I did not find literature data on such density-dependent effects in other predator–prey systems. In the case of Jeschke and Tollrian, the predators were 4th-instar *Chaoborus obscuripes* larvae (Diptera) and the prey *Daphnia pulex* (Crustacea), which can inducibly defend themselves against *Chaoborus* spp. and other invertebrate predators: in the presence of such predators, *D. pulex* transforms from the typical morph to the defended morph that has neckteeth on its carapace (Tollrian, 1993; Tollrian and Dodson, 1999). This defense lowers *Chaoborus* attack efficiency and is thus a step 5 defense (Havel and Dodson, 1984). For general treatises of inducible defenses, see Karban and Baldwin (1997) and Tollrian and Harvell (1999a). The density-dependent

effects of the step 5 defense shown in Fig. 4 are the differences in predation risk or consumption rate, respectively, between 2nd-instar *Daphnia pulex* of the typical morph and the neckteeth morph. The differences in predation risk or consumption rate between 2nd and 3rd instars of the typical morph can be used to investigate the effects of a step 1 defense. Of course, this is not an example of a real defense, for the 3rd instars are simply at a different ontogenetic stage compared to the 2nd instars, and the nutritional value of 3rd instars is higher than that of 2nd instars, so the predator's energy intake is probably not decreased by this “defense”. Nonetheless, the empirical data allow a test of the predictions developed above for step 1 defenses because, as outlined by Jeschke and Tollrian (2000), the *Chaoborus* larvae had the same success rate on both instars, handling time was negligible, and digestion time was larger for 3rd-instar *Daphnia*. I am not aware of other empirical data that could be used to test the predictions for density-dependent effects of step 1 defenses.

In case of Esaias and Curl (1972), the predators were the copepods *Arcatia tonsa* and *Calanus pacificus* and the prey *Gonyaulax* spp. These dinoflagellates have been used in two different conditions, either with a low (undefended) or high (defended) capacity for bioluminescence. According to Esaias and Curl (1972), bioluminescence in dinoflagellates reduces the attack efficiency of copepods. It is thus a step 5 defense.

How do the empirical data relate to the simulation results? The effect of the *Daphnia* step 1 defense on predation risk is not large and no clear dependence on prey density can be observed. The latter is not in accordance to the theoretical predictions shown in Fig. 2. A possible explanation is that a step 1 defense has to be very strong in order to allow the detection of a clear dependence on prey density in empirical data. Note that the defense in the simulation underlying Fig. 2 increased digestion time by 150% but showed nonetheless no large absolute effect on predation risk. The empirical density-dependent effect of the step 1 defense from the predator's perspective agreed with the simulated effect: with increasing prey density, consumption rate was affected more strongly. The empirical effects of all three step 5 defenses agreed with the simulation results as well. From the prey's perspective, the change in predation risk was smaller at high prey density; from the predator's perspective, the change in consumption rate increased up to an intermediate prey density but decreased beyond. In conclusion, the reviewed empirical data generally support the simulation results presented above.

### 5.2. Costs and benefits of defenses and offenses

The results presented here can be used to investigate the prey densities at which the benefits of a defense or offense outweigh its costs and thus at which prey densities a constitutional defense or offense should evolve or a phenotypically plastic defense or offense should be

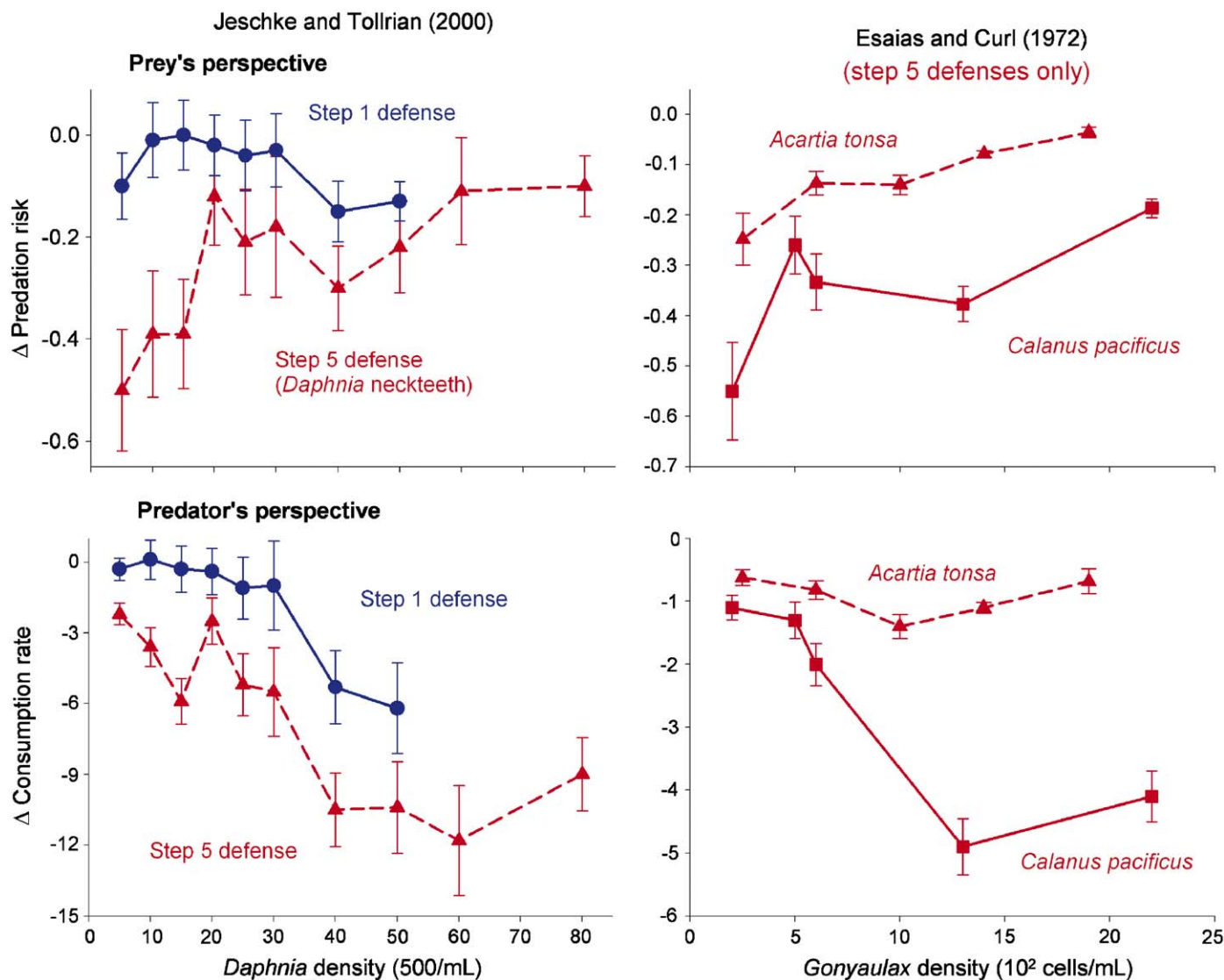


Fig. 4. Empirically observed density-dependent effects of prey defenses (means ± SE). Data are from Jeschke and Tollrian (2000) and Esaias and Curl (1972). See text for further details.

expressed. The main benefit of a defense is generally the reduction of predation risk. Reductions in addition to those shown in Fig. 2 are possible, e.g. due to predator switching to another prey or effects on predator–prey population dynamics (cf. Stephens and Krebs, 1986; Vos et al. 2004). Possible costs of defenses have been outlined by Tollrian and Harvell (1999b; see also Ruxton et al., 2004). Table 1 gives the analogous costs of offenses. The benefit of an offense is generally the increase in consumption rate, as shown in Fig. 3.

Let us assume that offense costs are independent of prey density. This assumption is certainly not strictly true, e.g. offense usage increases with increasing prey density and therefore, the total costs for offense usage, i.e. operation costs, increase with increasing prey density. On the other hand, offense costs should be less density dependent than offense benefits. Thus, assuming offense costs to be independent of prey density seems to be a reasonable

simplification. Let us imaginarily draw horizontal lines in the graph at the bottom of Fig. 3 that represent the costs of each type of offense. An offense's benefits outweigh its costs when  $\Delta$  consumption rate is above the horizontal line. We would therefore expect that constitutive step 1 offenses evolve or inducible step 1 offenses are expressed at high prey densities, and that step 2, 3, 4, 5 offenses evolve or are expressed at intermediate prey densities. Analogous considerations for defenses lead to the expectation that step 1 defenses are expressed at intermediate prey densities and that step 2, 3, 4, 5 defenses are expressed at low prey densities.

How do empirical findings relate to these theoretical considerations? Data from inducible defenses and offenses are especially useful here because they allow comparison of individuals that differ in the presence of the defense or offense, respectively, but are identical otherwise.

In case of inducible prey defenses, Wiackowski and Starońska (1999) showed that the expression of a step 5

Table 1  
Potential costs of predator offenses (cf. Table 17.1 in Tollrian and Harvell, 1999b, for costs of prey defenses)

(1) Allocation costs	
(a) Construction costs	Resources and energy needed for building the offense, e.g. for a web-spinning spider: resources and energy additionally needed for building a larger web
(b) Maintenance costs	Resources and energy needed for maintaining the offense, e.g. for a web-spinning spider: resources and energy additionally needed for maintaining a larger web
(c) Operation costs	Resources and energy needed for using the offense, e.g. for an eagle: resources and energy additionally needed for using sharper eyes
(2) Opportunity costs	E.g. another offense would be more efficient
(3) Environmental costs	E.g. the offense increases the probability that the consumer is preyed upon by its own predators

defense by *Euplotes octocarinatus* against *Stylonychia mytilus* (both are ciliates) decreased with increasing *Euplotes* density. This finding is in accordance with the expectations developed above and was reproduced by Tollrian et al. (submitted) in six other aquatic predator–prey systems.

Inducible predator offenses in the broad sense include the regulation of searching activity depending on prey density. For example, Hirvonen (1999) has shown that with increasing prey density, larval damselflies (*Lestes sponsa*) feeding on *Daphnia magna* first increase searching activity, then reach a maximum value, and finally decrease searching activity again. Because increasing or decreasing searching activity means switching on or off a step 2 offense, respectively, Hirvonen's results are consistent with the theoretical expectations. Similar examples for predators regulating searching activity as a response to a change in prey density have been given by Parsons et al. (1967), Ohman (1984), Plath (1998), and others. Besides behavioral inducible offenses, consumers also have developed morphological inducible offenses. For example, Wikelski and Thom (2000) have shown that marine iguanas (*Amblyrhynchus cristatus*) shrink as a response to low plant abundance. Since gut capacity is related to body size (Calder, 1996), this shrinking can be interpreted as “switching off” a step 1A offense at a low food abundance. When food abundance is high again, the iguanas regrow to their former size, i.e. they are equipped with their offense again. This pattern is in accordance to the expectations developed above. Similarly but more suddenly, Burmese python (*Python molurus*) and other predators adapted to infrequent meals build and rebuild their gut when they are feeding or starving, respectively (Starck and Beese, 2001), again in accordance with the expectations. For further morphological inducible offenses, see Padilla (2001), Kopp and Tollrian (2003a, b), and references therein. Finally, Jeschke et al. (2004) expected on the basis of theoretical considerations that a filter-feeding foraging strategy compared to non-filter feeding is adaptive at intermediate prey densities. The empirical observations from the literature Jeschke et al. reviewed are in line with this expectation.

### 5.3. Outlook

Apparently, the SSS equation (Jeschke et al., 2002) is a helpful tool for classifying prey defenses and predator offenses into different types and for predicting their

density-dependent effects. The equation thus helps to predict under which conditions defenses and offenses will evolve or, if they are phenotypically plastic, under which conditions they are expressed.

In the present study, only all-or-nothing defenses and offenses were considered. It would be interesting and more realistic to ask what kind of constitutive offense or defense should evolve or to which degree an inducible offense or defense should be expressed, e.g. to which degree a neckteeth defense should be expressed by a *Daphnia pulex* (cf. Tollrian, 1993). The most promising approach to these questions is probably an ESS model that looks not only at the density-dependent effects of defenses and offenses but also at frequency dependence.

Another important extension of this study will be the consideration of different predator densities. While generalist predators are not strongly affected in their density by the expression of a defense in one of their prey species, specialist predators often are. From an evolutionary perspective, prey defenses diminish the growth of predator populations and will thus also benefit related individuals. Such effects may be analysed by means of a predator–prey population dynamics model that includes the SSS equation as the functional response model. It could be analysed theoretically and then parameterized for real systems. The latter would take advantage of the mechanistic power of the SSS equation.

The consideration of heterogeneous environments with predators aggregating, and possibly interfering, in high-quality patches will be a further extension. Jeschke et al. (2002) reviewed theoretical models that consider such effects. Due to the modular nature of the SSS equation, it will be relatively straightforward to extend the model accordingly. An alternative approach has been offered by Arditi and Ginzburg (1989), who proposed to replace prey density by the ratio of prey-to-predator density. For example, imagine two patches, one with a prey density of 50 and a predator density of 5, the other one with a prey density of 80 and a predator density of 10. The prey-to-predator ratios are 10 and 8, respectively. These ratios can simply be included in the model presented here if one wants to follow the ratio-dependent approach. There has been a long-standing debate between proponents of classical prey dependence (reviewed in Jeschke et al., 2002) and proponents of ratio dependence (Diehl et al., 1993; Abrams

and Ginzburg, 2000). The model presented here is suitable for extension by both schools of thought.

These proposed future steps may be helpful for basic evolutionary ecologists because they allow a better understanding of the ecology and evolution of defenses and offenses. The steps may also be helpful for applied evolutionary ecologists, e.g. in the context of invasive species where the EICA hypothesis proposed by *Blossey and Nötzold (1995)* “predicts that once an organism escapes its natural enemies, it no longer needs the defenses it had evolved against them.” (*Withgott, 2004*). In terms of the present study, the defense of such an organism does not have a benefit anymore. Although we need to take further steps before applying the considerations presented here to invasive species theory, this goal seems not too far away.

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