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Density-dependent effects of prey defences

Abstract In this study, we show that the protective advantage of a defence depends on prey density. For our investigations, we used the predator-prey model system *Chaoborus-Daphnia pulex*. The prey, *D. pulex*, forms neckteeth as an inducible defence against chaoborid predators. This morphological response effectively reduces predator attack efficiency, i.e. number of successful attacks divided by total number of attacks. We found that neckteeth-defended prey suffered a distinctly lower predation rate (prey uptake per unit time) at low prey densities. The advantage of this defence decreased with increasing prey density. We expect this pattern to be general when a defence reduces predator success rate, i.e. when a defence reduces encounter rate, probability of detection, probability of attack, or efficiency of attack. In addition, we experimentally simulated the effects of defences which increase predator digestion time by using different sizes of *Daphnia* with equal vulnerabilities. This type of defence had opposite density-dependent effects: here, the relative advantage of defended prey increased with prey density. We expect this pattern to be general for defences which increase predator handling time, i.e. defences which increase attacking time, eating time, or digestion time. Many defences will have effects on both predator success rate and handling time. For these defences, the predator's functional response should be decreased over the whole range of prey densities.

Key words *Chaoborus obscuripes* · *Daphnia pulex* · Density dependence · Functional response · Inducible defences

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Introduction

Most organisms form defences against predators (we define the term predator in a broad sense, i.e. including carnivores, herbivores, parasites, and parasitoids). Such defences reduce the predator's prey uptake, or from the prey's point of view: they reduce predation risk (number of prey eaten divided by prey density). This protective advantage of a defence probably varies with prey density, and since prey density in natural environments will rarely be constant, information about density dependence is essential to understand the function and the evolution of defence systems (see Baldwin 1996).

For our study, we took advantage of special properties of inducible defence systems. They allow the precise calculation of defence effects, because otherwise identical (even at the genetic level in our system) animals, with and without defences, can be compared. Inducible defences have been reported from diverse organisms [recently reviewed in Karban and Baldwin (1997) and Tollrian and Harvell (1999)].

We studied density-dependent effects in the predator-prey model system *Chaoborus obscuripes-Daphnia pulex. Chaoborus* larvae (Diptera) live in freshwater ponds and are mainly nocturnal and tactile ambush predators (Duhr 1955; Teraguchi and Northcote 1966; Giguère and Dill 1979; Smyly 1979; Riessen et al. 1984). When exposed to chemicals released by *Chaoborus* larvae, juveniles of the water-fleas *Daphnia pulex* (Crustacea) build pedestals on the dorsal carapace with associated spines called neckteeth (Krueger and Dodson 1981; Tollrian 1993). In combination with other protective features (Spitze and Sadler 1996), this inducible defence effectively reduces the predation rate (Krueger and Dodson 1981; Tollrian 1995; reviewed in Tollrian and Dodson 1999). Studying the underlying mechanism of this defence, Havel and Dodson (1984) found higher escape probabilities after body contact with *Chaoborus* for daphnids with neckteeth. To examine density-dependent effects, we compared predation rates of *Chaoborus obscuripes* for neckteeth-defended *Daphnia* with predation

rates for undefended *Daphnia* over a range of prey densities in separate feeding experiments.

Density-dependent effects of predation can be characterized by the functional response of a predator, which can most easily be described by the two variables *a* and *b* (Holling 1959):

$$y(x) = \frac{atx}{1+abx}, \quad \text{Holling's disc equation} \qquad (1)$$

where *a*=success rate, *b*=handling time per prey item, *t*=experimental time, *x*=prey density, and *y*=no. of prey eaten. The disc equation simulates a type II functional response which is a hyperbolic curve. The curve's gradient in the origin is equal to *at*, and the asymptotic maximum for *x*→∞ is *t/b*. In other words: according to the disc equation, the functional response of a predator at low prey densities is mainly defined by the predator's success rate, whereas at high prey densities it is mainly defined by the predator's handling time. Success rate *a* is the product of four components: (1) encounter rate, (2) probability of detection, (3) probability of attack, and (4) efficiency of attack. A synonym for the predator-oriented term "success rate" is the prey-oriented term "vulnerability". Handling time *b* describes the effect of prey density on predation rate. It includes time spent for attacking, eating, and digesting prey (Holling 1966).

We used our system to study effects of two different types of defences: (1) defences which decrease success rate, and (2) defences which increase handling time.

1. The neckteeth defence decreases the efficiency of attack (Havel and Dodson 1984) and thus decreases success rate *a*. This results in a decreased prey uptake at low prey densities. Since success rate does not limit maximum prey uptake (when prey density is high enough), at very high densities there should be no difference between predation rates on neckteeth-defended and undefended prey. As a consequence, the relative advantage of defended prey over undefended prey should be greatest at low prey densities and should gradually decline as density increases.
2. Defences which increase handling time do not prevent ingestion. They are therefore not adaptive in typical predator-prey systems where predator attacks are lethal for the prey. However, they *are* adaptive in systems where an initial attack is not lethal and the individual prey itself can benefit (e.g. in herbivore-plant systems). We experimentally simulated the density-dependent effects of this type of defence by comparing the functional responses of *Chaoborus* to two size classes of *D. pulex* which had similar vulnerabilities, but which differed in body mass. The difference in body mass led to a difference in digestion time and thus in handling time. Normally, bigger prey not only increase handling time but also affect other components of the predation cycle. However, in the *Chaoborus-Daphnia* system differently sized prey can have similar vulnerabilities, because encounter rate increases with prey size whereas efficiency of attack

decreases with prey size, leading to a dome-shaped vulnerability-size function (Pastorok 1981). According to the disc equation, an increased handling time should result in an increasing relative advantage with increasing prey density. The advantage should rise to an asymptotic value, defined by the maximum prey uptake of both defended and undefended prey. In other words: the relative advantage should increase with prey density and should remain constant at prey densities on the plateaus of the two functional response curves.

Materials and methods

Organisms

As predators we used fourth instar larvae of *Chaoborus obscuripes*, which is a large species of the genus *Chaoborus* [length 11.59±0.057 mm (mean±SE), *n*=180]. The larvae were caught in a fishless pond in Langenbach near Munich and kept in a dark climate-controlled room (4°C). As prey we used the clone *Daphnia pulex* R9, which has also been used in previous studies (Tollrian 1993, 1995). We cultured this clone at 20°C in an artificial medium: 1.11 l medium consisted of 700 ml tap water, 400 ml ultrapure water, and 10 ml SMB medium [for SMB medium see Miyake (1981)]. We used the same medium for the experiments. The water-fleas were fed daily, ad libitum, with *Scenedesmus obliquus*.

We used three different types of prey: (1) second juvenile instar *D. pulex* of the typical morph (2 TM); (2) second juvenile instar *D. pulex* of the neckteeth morph (2 NM); and (3) third juvenile instar *D. pulex* of the typical morph (3 TM). Since second instar juveniles carry the biggest neckteeth (Tollrian 1993) and suffer the highest predation (Tollrian 1995), we chose this instar to study the effects of neckteeth. Typical and neckteeth morph daphnids did not differ in size (means±SE): 823±11.5 µm (*n*=26) for 2 TM, 825±7.1 µm (*n*=25) for 2 NM. There is no indication that the neckteeth defence per se influences *Chaoborus* digestion time. We therefore assume that *Chaoborus* digestion time mainly depends on *Daphnia* body size and, thus, should be equal for neckteeth-defended and undefended *Daphnia*. For *Chaoborus* larvae, digestion time is the most important component of handling time, as both attacking and eating times are relatively short: digestion time=several hours (Giguère 1986), attacking time ≤0.003 s, eating time≈15 s (Pastorok 1981). Consequently, *Chaoborus* handling time can be assumed to be equal for neckteeth-defended and undefended *Daphnia*.

To experimentally simulate the effects of a defence which increases digestion time, we compared typical second and third instars (1071±16.0 µm, *n*=25) of *D. pulex*. Third instars have a larger body size but very similar vulnerabilities to second instars (see Results).

To obtain the experimental animals we isolated cohorts of 30 to 40 juvenile *D. pulex* which were born on the same day and reared them in 5-l beakers. Since the first two clutches of daphnids consist of smaller and more size-variable neonates (Ebert 1993), we only used juveniles from third and subsequent clutches. To obtain water-fleas with neckteeth, we additionally placed net cages into half of the beakers. We placed 20 *C. obscuripes* into each net cage and fed them daily with 60±10 *D. pulex*. This *Chaoborus* density ensured maximal neckteeth induction (Tollrian 1993).

Two days before starting an experiment, we transferred predators from the cold storage room to the experimental room for acclimatization. We fed the larvae prior to each experiment because using pre-starved chaoborids would have resulted in an overestimation of feeding rates (Spitze 1985). We isolated the predators 11 h before starting an experiment, to avoid over-stimulation of their mechanoreceptors and to simulate a diel feeding pause. We performed experiments with single predators in 2-l beakers

filled with 500 ml medium with algae and a defined number of daphnids. Predation experiments at each density were replicated 5 or 10 times. The feeding trials lasted 12 h and were performed in the dark, at night. Temperature was recorded with a thermograph [20.25 ± 0.06°C (mean$\pm$SE), $n=245$]. At the end of an experiment, we removed the predator and counted all remaining live and dead daphnids.

We used a total of 9225 *D. pulex*, and found 132 (1.43%) dead but not eaten after the experiments. The type of prey had no influence on the number of uneaten dead daphnids (two-way ANOVA: "prey", $P=0.69$, $F_{2, 217}=0.37$, interaction "prey$\times$density", $P=0.85$, $F_{16, 217}=0.64$; SPSS for Windows 8.0, SPSS). To avoid overestimation of prey consumption, we counted uneaten dead water-fleas as surviving prey.

Analysis

We analysed the functional response data with logistic regression (Trexler et al. 1988; Hosmer and Lemeshow 1989; Juliano 1993; Trexler and Travis 1993; Sokal and Rohlf 1995; Hardy and Field 1998). We performed three blocks of logistic regression analyses. First, we calculated estimated functional response curves. Here, the independent variable was "prey density" and the dependent variable was the variable "eaten" (1=individual was eaten, 0=individual survived). We started with estimating the appropriate scale (normal, squared, or cubed) for the variable "prey density" (Hosmer and Lemeshow 1989). For all three types of prey, it was not necessary to use squared or even cubed prey densities. After performing logistic regression for each type of prey, we calculated estimated functional responses as estimated predation risks multiplied with prey density. Second, we calculated *estimated* relative advantages of the two types of defence. Here, we used four independent variables: "prey density", "type of prey", and the two interaction variables "density$\times$2 NM" and "density$\times$3 TM". The dependent variable was the variable "survived" (1=individual survived, 0=individual was eaten). Finally, we calculated 95% confidence intervals and *P*-values for the *observed* relative advantages separately for each prey density with the independent variable "type of prey" and the dependent variable "survived". We defined the relative advantage of defended prey as the odds ratio of survival for defended against undefended prey=(number of defended prey survived/number of defended prey eaten)/(number of undefended prey survived/number of undefended prey eaten). An odds ratio >1 means an advantage, an odds ratio equal to 1 means no advantage, and an odds ratio <1 means a disadvantage (Sokal and Rohlf 1995).

Results

D. pulex with neckteeth had a distinctly lower predation risk compared to typical *D. pulex* (Fig. 1). The estimated relative advantage for neckteeth morphs at a density equal to 0 was 3.58 (99.9% confidence interval, 2.40–5.34; Table 1), so the neckteeth significantly reduced *Chaoborus* success rate. This relative advantage was significantly decreasing with increasing prey density (Table 1, interaction term "2 NM$\times$density", $P<0.001$). Nevertheless, the relative advantage remained significant, even at very high prey densities (all $P<0.001$, except for 20 *Daphnia*/500 ml, $P<0.05$; Fig. 2a).

Both age classes of typical morphs of *D. pulex* had similar vulnerabilities (Figs. 1, 2b; Table 1). The relative advantage for the third instar increased with prey density (interaction term "3 TM$\times$density" in Table 1, $P<0.05$). The difference in predation rates was significant only for
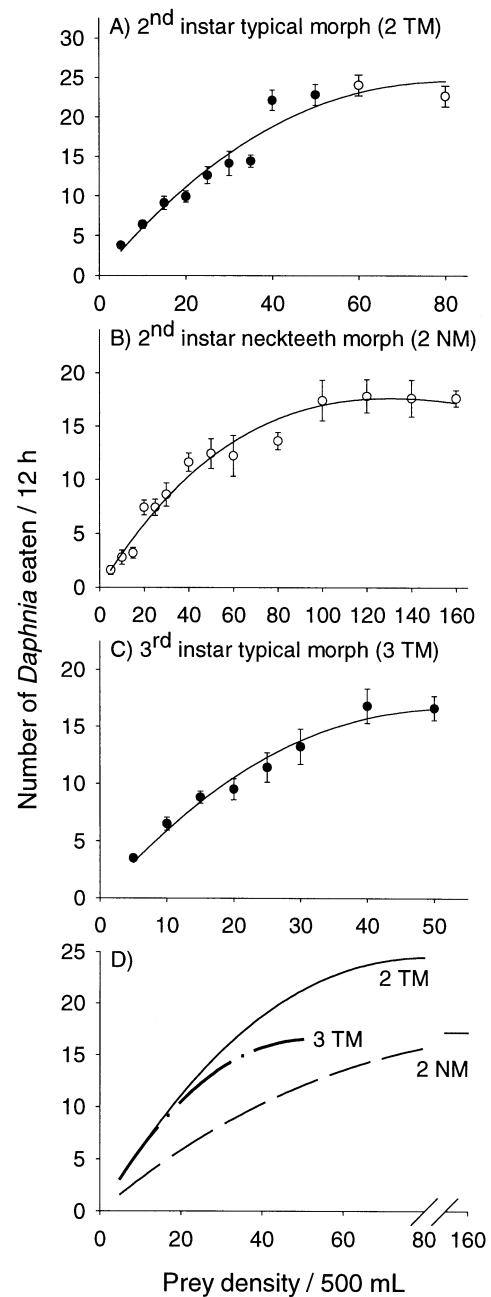

Fig. 1 The functional responses of *Chaoborus obscuripes* to *Daphnia pulex*. *Circles* represent means ($\pm$SE), *filled circles* indicate ten replicates, *open circles* indicate five replicates. *Lines* are fitted functional response curves using logistic regression analyses. For the second juvenile instar of *D. pulex* of the typical morph (*2 TM*), $y=[\exp(0.5690-0.0174x)\times x]/[1+\exp(0.5690-0.0174x)]$; for the second juvenile instar of *D. pulex* of the neckteeth morph (*2 NM*), $y=[\exp(-0.7059-0.0088x)\times x]/[1+\exp(-0.7059-0.0088x)]$; for the third juvenile instar of *D. pulex* of the typical morph (*3 TM*), $y=[\exp(0.6419-0.0270x)\times x]/[1+\exp(0.6419-0.0270x)]$; where $x=$ prey density and $y=$ number of prey eaten. Note that abscissas as well as ordinates have different scales

Table 1 Results of overall logistic regression analysis, dependent variable "survived". Model fit: Hosmer-Lemeshow test C=11.63, 8 df, P=0.17]. Note, b is a statistical term of the logistic regression analysis; it is different from the handling time b in the disc equation (Eq. 1). *2 TM* Second juvenile instar of *Daphnia pulex* of the typical morph, *2 NM* second juvenile instar of *D. pulex* of the neckteeth morph, *3 TM* third juvenile instar of *D. pulex* of the typical morph

Variable	b	SE(b)	exp(b)	P-value[a]
Constant (=2 TM)	–0.5690	0.0866		
2 NM	1.2755	0.1216	3.5806	***
3 TM	–0.0729	0.1486	0.9297	n.s.
Density	0.0174	0.0019		
2 NM×density	–0.0085	0.0021	0.9915	***
3 TM×density	0.0096	0.0039	1.0097	*

*P<0.05, ***P<0.001, *n.s. P≥0.05
[a]P-values for exp(b) indicate significant deviation from 1
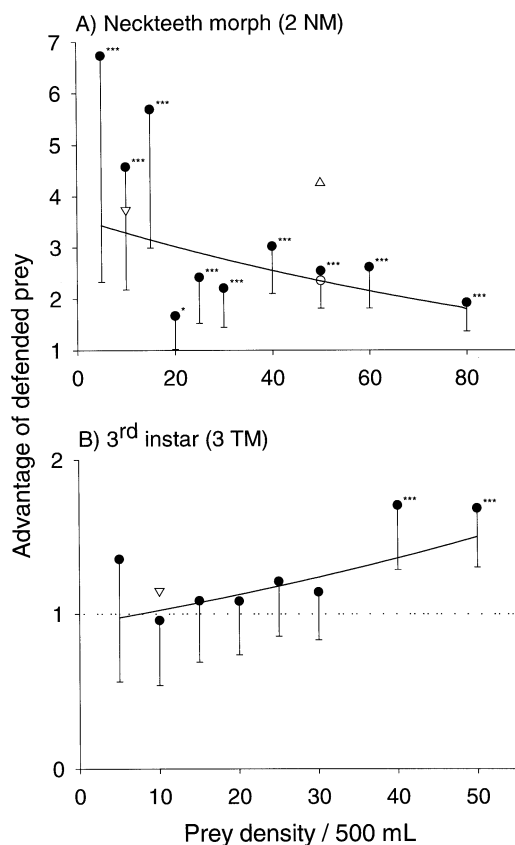

Fig. 2A,B Density-dependent relative advantages of defended prey. The relative advantage is the odds ratio of survival for defended against undefended prey. * indicate significant advantages, i.e. significant deviation from a value of 1 (*P<0.05, ***P<0.001). *Filled circles* represent means (–95% confidence interval), *solid lines* are logistic regression lines: **A** 2 NM, y=exp(1.2755–0.0085x); **B** 3 TM, y=exp(–0.0729+0.0096x); where x=prey density and y=advantage of defended prey. *Open triangles pointing down* indicate data from Tollrian (1995) {predator: *Chaoborus crystallinus*; difference in length (Dl)=[(length of neckteeth morph–length of typical morph)/length of typical morph]× 100%=0%}. *Open triangles pointing up* indicate data from Parejko (1991) (*Mochlonyx* sp.; Dl=4.45%). *Open circles* indicate data from Krueger and Dodson (1981) (*Chaoborus americanus*; Dl=9.38%). Note that abscissas as well as ordinates have different scales. For abbreviations, see Fig. 1

the two highest prey densities tested: 40 and 50 *Daphnia*/500 ml (both P<0.001; Fig. 2b).

All three types of prey gave rise to type 2 functional response curves (see Fig. 1) (Holling 1959, 1966). However, the functional response curve of typical morph daphnids reached its plateau at lower prey densities than the functional response curve of neckteeth morph daphnids. The observed mean maximum numbers of prey eaten were: 24 (prey density 60/500 ml) for 2 TM; 17.8 (prey density 120/500 ml) for 2 NM; and 16.8 (prey density 40/500 ml) for 3 TM.

Discussion

Neckteeth – defences which decrease success rate

Neckteeth morph daphnids suffered clearly lower predation rates than typical morphs. So far, all comparable studies have established an advantage for neckteethmorph water-fleas (Fig. 2a). The quantitative differences between the data obtained in these studies may have been due to the different sizes of the predator species used.

Natural densities of daphnids mostly lie in those regions that we call "low prey densities" (e.g. Dodson 1972). At these densities, our results were in accordance with the hypothesis: Defended prey had a clearly lower vulnerability. However, in contrast to our expectations, we observed a relative advantage of defended *Daphnia* at high prey densities where the plateau of the functional response curve was already reached. To offer an explanation, it might be tempting to assume that, beside the decrease in success rate, handling time was also increased by the neckteeth. E.g. Abrams (1990) pointed out that the parameter b is increased by the average time spent on unsuccessful attacks. However, this effect should be negligibly small for *Chaoborus*. The attack of a *Chaoborus* larva only lasts up to 0.003 s (Pastorok 1981). Thus, an increase in attacking time would be negligible in comparison to the digestion time which lasts several hours (Giguère 1986). This argument also holds for eating time. For *Daphnia* of the size we used in our experiments, *Chaoborus* eating time is only about 15 s

(Pastorok 1981). As a consequence, a possible increase in eating time would not have a significant effect on handling time. The third and last component of handling time is digestion time. There is no reason to assume that a *Chaoborus* larva needs more time to digest a defended compared to an undefended *Daphnia*. To sum up, there was no indication that neckteeth defence notably affected *Chaoborus* handling time. But why did the relative advantage of defended *Daphnia* remain at high prey densities? There are two possible explanations:

1. High prey densities could have caused predator confusion. In other experiments, we have shown that a confusion effect is present in the *Chaoborus-Daphnia* system (unpublished data). For example, at a prey density of 5 *Daphnia*/500 ml, the average attack efficiency of a predator was 43%, and for 160 *Daphnia*/500 ml it was only 33%. At high densities where the functional response for the defended morph should reach the same plateau as the functional response for the typical morph, a confusion effect and the defence could act synergistically. To illustrate this, we computed hypothetical functional response curves that would arise without a confusion effect, i.e. if success rate remained constant at all prey densities. For this, we used the Gause-Ivlev equation (Gause 1934; Ivlev 1961):

$$y=k \times [1-\exp(-ax)], \tag{2}$$

where a=success rate, k=maximum number of prey eaten, x=prey density, and y=number of prey eaten; $k \approx 30$, $x=5$, $y_{TM}=3.45$, $y_{NM}=1.44$ (experimental data) $\Rightarrow a_{TM} \approx 0.03$, $a_{NM} \approx 0.012$. Without confusion, the relative advantage of neckteeth morphs would decrease with prey density and would become negligible at very high densities (Fig. 3). This simulation suggests that a confusion effect is a potential explanation.

2. A special feeding characteristic of *Chaoborus* could also be responsible for the remaining advantage. *Chaoborus* larvae do not feed continually but in discrete feeding intervals. A larva can pack several prey items into its pharynx before it makes a digestive pause, which can last several hours (Smyly 1979). The lower success rate may lead to a time delay in crop filling. This is a possible explanation for the step-like form of the functional response curves (Fig. 1). A consequence may have been that with typical prey the larvae were already in the next feeding interval, while with defended prey they were still in the digestive pause. The duration of the predation experiments would then decide whether or not the same plateau will be reached.

Third instar prey-defences which increase handling time

The comparison of the two typical morph instars of *D. pulex* had two main results. First, functional responses were similar for both instars at low prey densities, prov-
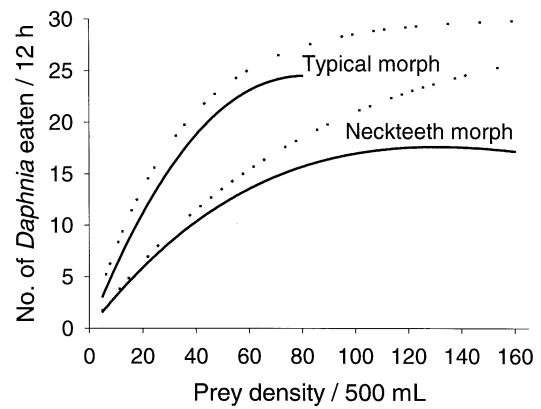

Fig. 3 In this study, the relative advantage of neckteeth-morph *Daphnia* remained significant at very high prey densities. A possible explanation is predator confusion. The observed functional response curves (*solid lines,* fitted with logistic regression analyses; see Fig. 1) are compared with hypothetical curves which would result if there was no confusion effect [*dotted lines*; equations: Gause (1934), Ivlev (1961)]: $y=30 \times [1-\exp(-0.03x)]$ for *typical morph*, $y=30 \times [1-\exp(-0.012x)]$ for *neckteeth morph*. Without a confusion effect, the difference between the functional responses for typical and neckteeth morph would lose significance at high densities

ing that, although both instars had different sizes, they had similar vulnerabilities. Second, the larger third instar had an increasing relative advantage with increasing prey density. This was in accordance with results from Krylov (1992), Spitze (1985), and Vinyard and Menger (1980), who found similar relationships in other *Chaoborus-Daphnia* systems. This is also known from other predator-prey systems, e.g. *Ischnura-Daphnia* (Thompson 1975), *Notonecta-Culex* (Fox and Murdoch 1978), and *Didinium-Paramecium* (Hewett 1980). The reason is obvious: a predator needs more time to digest larger prey. This results in a lower predation rate for larger prey at high densities. It should be noted that a decreased prey uptake is only disadvantageous for a predator when total energy gain is lower. In our study, the decreased prey uptake was presumably not a disadvantage for the predators since a third instar *Daphnia* provides more energy than a second instar one. In summary, this defence did not affect success rate, only digestion time, giving rise to a relative advantage which increased with prey density.

Conclusions

A lower functional response curve for defended prey is common. This reduction can be based on different types of defence:

Defences which reduce success rate

The success rate can be reduced by: (1) a reduced encounter rate, e.g. predator avoidance; (2) a reduced probability of

detection, e.g. camouflage; (3) a reduced probability of attack, e.g. aposematic coloration; or (4) a reduced efficiency of attack (as in this study). Our results show that for these defences the relative advantage of defended prey is highest at low prey densities and decreases with prey density.

Defences which increase handling time

Such defences can, for example, be achieved in plants by incorporation of unpalatable or non-digestible substances. We expect that defences which increase handling time usually evolve in predator-prey systems where attacks are not lethal, e.g. in many herbivore-plant systems. In these systems, the individual prey itself benefits from its defence. Our experimental simulation indicates that the relative advantage of such defences increases with prey density.

However, defences which reduce success rate will frequently additionally increase handling time, e.g. escape reactions decrease attack efficiency and increase attacking time, and armoured structures decrease attack efficiency and often increase eating time. How the predator's functional response is influenced by these combined effects depends on the specific properties of the defence system itself.

With this study we want to emphasize that all defences which are not 100% protective are density-dependent in their effects on predators and prey. It is therefore essential to integrate these effects in predator-prey models, for example, cost-benefit models of defences.

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