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A trophic polymorphism induced by both predators and prey

B.R. Schmidt,[1,2]* N. Ramer[1]‡ and J. Van Buskirk[1]

[1]Zoologisches Institut, Universität Zürich, Winterthurerstrasse 190, 8057 Zürich and
[2]KARCH, Passage Maximilien-de-Meuron 6, 2000 Neuchâtel, Switzerland

ABSTRACT

Problem: We tested whether plasticity in head shape of newt larvae represents a predator-induced resource polymorphism that may allow newts to compensate for costs of defence.

Organism: Larvae of European *Triturus* newts exhibit defensive behaviour and morphology when in ponds with predators. Predator-induced newt larvae also have large heads, although head shape does not have a direct influence on vulnerability to predation.

Methods: We surveyed the morphology and diet of *T. alpestris* larvae in 17 natural ponds. A laboratory experiment was used to assess the effects of predators and food size on trophic morphology.

Results: In natural ponds, individuals with relatively large heads had large prey, and a larger volume of prey, in their guts. In the experiment, a large head was induced by both prey size and predator cues, acting additively.

Conclusion: Even though the large head offers no protection from predation, it is directly induced by predators and enables newts to consume more profitable prey.

Keywords: inducible defence, morphology, phenotypic plasticity, prey size, resource polymorphism, *Triturus*.

INTRODUCTION

Developing defences against herbivores, predators, and disease is known to be costly. Costs may arise from trade-offs between resistance to enemies and other functions such as resource acquisition, or from unfavourable changes in interactions with other organisms (DeWitt *et al.*, 1998; Heil and Baldwin, 2002; Strauss *et al.*, 2002). In fact, costs are the main reason why many defences are inducible rather than permanent (Tollrian and Harvell, 1999). High costs of defence suggest that selection will favour mechanisms that decrease them (Lenski, 1988; Simms, 1992). In some cases, however, it is difficult to envision how costs can be reduced. The inescapable time–allocation trade-off between avoiding predators and feeding is often cited in this

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* Address all correspondence to B.R. Schmidt, Zoologisches Institut, Universität Zürich, Winterthurerstrasse 190, 8057 Zürich, Switzerland. e-mail: bschmidt@zool.unizh.ch

‡ *Present address*: Praktischer Umweltschutz Schweiz, Hottingerstrasse 4, Postfach 211, 8024 Zürich, Switzerland.

context: time spent hiding from predators simply cannot be devoted to foraging (Lima, 1998). This trade-off is fundamental to the theory of predator–prey interactions (Abrams, 2000), in part because of its inevitability.

We propose that costs of responding to enemies might be reduced, if not avoided entirely, by compensatory changes in other traits that have no direct defensive function. Even the well-known predator avoidance–growth rate trade-off could be circumvented if animals compensated for lost foraging time by improving digestive efficiency, increasing consumption rates while feeding, or enlarging diet breadth. Under this scenario, predators might induce more than simply costly defensive traits in their prey – they could also induce traits that enhance resource acquisition to compensate for the costs. Here we report a predator-induced shift in the trophic morphology of newt larvae that is associated with increased feeding success, and may therefore be a mechanism that allows prey to reduce the overall cost of defence against predation.

The larvae of *Triturus alpestris* newts (Amphibia: Urodela) exhibit an inducible defence similar to that found in many larval amphibians: they shift microhabitat use to avoid encountering predators and develop deeper tail fins to resist attacks (Van Buskirk and Schmidt, 2000; Orizaola and Braña, 2003; Schmidt and Van Buskirk, 2005). However, predation risk is also associated with a change in head shape quite unlike anything observed in other amphibians. *Triturus alpestris* develops a relatively broad and deep head when in ponds with predators, although this shift has no influence on vulnerability to predation (Van Buskirk and Schmidt, 2000). The relationship between predators and head shape is evident both in experiments and in nature, where head shape covaries with predation risk (Van Buskirk and Schmidt, 2000). Because gape size determines the dimensions of prey that can be captured and consumed (Smith and Skúlason, 1996; Maerz *et al.*, 2006) and larger prey are known to be more profitable (Ranta and Nuutinen, 1985), it is possible that the head response is a predator-induced mechanism of cost reduction. The present study tests this hypothesis experimentally and with a field survey. In the experiment, we ask whether developmental plasticity in head shape is induced by predators, by large prey in the diet, or by a combination of the two. Our hypothesis would be supported if predators directly induce plasticity in head shape. In the field survey, we addressed an assumption of our hypothesis – that newt larvae with relatively large heads capture larger prey. Taken together, the two kinds of results provide convincing evidence that predators induce changes in traits that are not defensive but that affect foraging success. Hence, predator-induced developmental plasticity in trophic morphology may serve to compensate for the costs of anti-predator responses.

METHODS

Relationship between head shape and diet

We used field data to test the assumption that variation in head shape affects the foraging of newt larvae, including their overall prey consumption and ability to swallow large prey. Diet and head morphology of *Triturus alpestris* were surveyed in 17 ponds in northern Switzerland during June 2000. Ramer (2001) provides exact locations of the ponds and full details of field methods. Briefly, we used dip nets and bottle traps to collect and preserve 266 newt larvae (10–24 per pond). To assess diet, we sorted stomach contents into taxa, counted the minimum number of individuals consumed, and measured the body length and width of the first 15 individuals of each taxon. We used length and width measurements to estimate prey volume based on the assumption that each animal was a cylinder. In all, 30 prey taxa were observed in our samples, the most abundant of which were cyclopoid copepods, *Daphnia*, ostracods, and chironomid larvae (Ramer, 2001). The morphology of larval newts was quantified by digitizing the coordinates of 31 landmarks in three-dimensional space (Van Buskirk and Schmidt, 2000) and calculating two linear distances between pairs of landmarks: head width and head depth. Body size was defined as the square root of centroid size, calculated from all landmarks excluding the tail tip (Bookstein, 1991).

We tested whether newt larvae with heads that were large relative to their body size consumed more prey or larger prey than expected for their body size. The two morphological measurements, prey size and prey quantity, were regressed against newt body size and body size squared, and the residuals were retained for further analysis. Correcting prey size and quantity for variation in newt body size was necessary because large newts contained far more and larger prey than small newts. The influence of head shape on prey size and volume was estimated from multiple regressions of the size-corrected size and quantity of prey on the relative width and depth of the head. Both models included pond as a random effect, and were implemented using Proc Mixed in SAS version 8.1 (SAS Institute, 1999).

Effects of predator cues and food size on head shape

We performed an experiment to determine if plasticity in head shape is induced by the size of prey or directly by predation risk. The experiment had a complete factorial design, with two levels of predation risk crossed with two levels of prey size. We repeated the entire design in two different years, with 10 replicates each in 2000 and 2001. Animals were raised individually in 0.1-m^2 plastic tubs containing 6 litres of water, arranged in a rectangular array in an outdoor aviary. The tubs were sheltered from rain, but were otherwise exposed to natural variation in environmental conditions. We placed five leaves into each tub to provide shelter, and maintained water levels by adding aged tap water whenever necessary. Larvae came from eggs deposited in captivity by adult newts collected in a pond near Zürich, Switzerland. About 10 males and 10 females contributed offspring, and we added larvae to the experiment 1–5 days after hatching.

Predation risk was manipulated three times per week by adding to each tub 100 ml of water drawn from a container in which an *Aeshna* dragonfly larva was either present or absent. The dragonfly consumed 300 mg of a 3 : 1 mixture of anuran tadpoles and *Triturus* larvae just prior to water transfer. Tubs in the no-predator treatment received 100 ml of water from a container without dragonflies. We reinforced the predator cue late in the experiment by placing a dragonfly larva, held within a cage, directly into a quarter of the tubs in the predator treatment. Caged dragonflies were rotated through the experiment every few days, and tubs in the no-predator treatment were outfitted with an empty cage.

We manipulated the size of prey by feeding newt larvae on *Daphnia* sp. of different sizes. All larvae consumed small *Daphnia* during the first 20 days. Thereafter, we sorted prey using sieves to create two treatments: newt larvae in the ‘small food’ treatment were fed *ad libitum* on *Daphnia* that passed through a 1-mm mesh, while those in the ‘large food’ treatment received *Daphnia* that were >1 mm or, late in the experiment, >1.4 mm. We added new food every 2–3 days.

The experiments ran for 46–52 days, from late June until mid-August, well before metamorphosis began. On the final day we photographed the larvae for morphometric analysis. In addition to the two head dimensions described above, we recorded tail length, tail depth, and tail muscle width (Van Buskirk and Schmidt, 2000).

We tested for effects of prey size and predator presence on head and tail shape of the newts using multivariate analysis of covariance followed by univariate analyses on individual traits. The two head dimensions were analysed separately from the body and tail traits, because the head was known in advance to be phenotypically plastic and was our focus of interest here. Independent variables included predator presence, prey size, their interaction, experiment (2000, 2001), and body size as a covariate. Figures were prepared with residuals from regressions of traits against experiment and body size.

RESULTS

Relationship between head shape and diet

Field-collected newt larvae with deep heads consumed larger prey and a greater volume of prey (Fig. 1). Multiple regression confirmed that individuals with relatively deep and narrow heads contained prey in their stomachs that were significantly larger than expected for their body size, and newt larvae with deep heads contained a relatively high volume of prey (Table 1).

Effects of predator cues and food size on head shape

In the experiment, both predator and food treatments influenced morphology of newt larvae (Fig. 2, Table 2). Multivariate analysis confirmed that the main influence of prey size was on the head: when fed large *Daphnia*, newt larvae developed wider and deeper heads. Predation risk induced a deeper tail fin and wider tail muscle. The influence of predators on head shape was not significant in the multivariate analysis, but univariate tests showed that larvae had relatively deep heads when in the presence of dragonflies. This same trait affected the size and the number of diet items in field-caught newts (Fig. 1). There were no interactions between the food and predator treatments.

DISCUSSION

Variation in the head shape of larval newts was associated with a resource polymorphism in nature: animals with relatively deep heads consumed larger prey and greater quantities of food overall. The experiment showed that this polymorphism was induced by both predation risk and prey size, acting additively. This represents a novel example in which predators directly induce a resource polymorphism. We argue that this response may have evolved under selection favouring a reduction in the costs of co-occurring with predators.

Resource polymorphisms are generally induced by diet (Smith and Skúlason, 1996), and we found that this is also true in *Triturus* newt larvae (Fig. 2). The impact of food size on head shape was significant in the multivariate analysis, and the same two head traits that were associated with feeding on large prey in natural ponds, relative head depth and width, were also significantly related to food size in the experiment. The mechanism by which large prey induce deep and wide heads presumably involves tissue growth in response to strain on the muscle and bones of the head imposed by regular consumption of large prey (Lanyon and Rubin, 1985; Day and McPhail, 1996). In this way, *T. alpestris* is similar to other amphibians for which diet

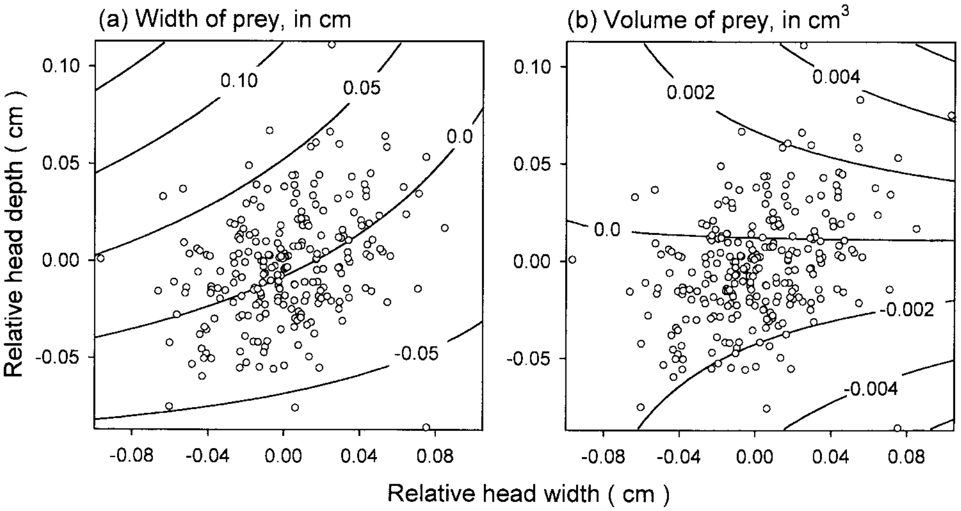

Fig. 1. Relationships between head shape and the size and amount of prey in the diets of *Triturus alpestris* larvae in natural ponds. Contours indicate the average body width of prey (a) or the total volume of prey (b) predicted from multiple regression. Each point represents an individual newt sampled from one of 17 ponds in northern Switzerland. Head morphology and prey size or volume are both residuals after regressions against the body size of the newt. Animals with relatively deep heads consumed prey that were large and numerous relative to body size.

Table 1. Multiple mixed-model regressions for effects of head shape on the size and quantity of benthic prey consumed by *Triturus alpestris* larvae sampled from 17 ponds in northern Switzerland (see Fig. 1)

	Average width of prey			Volume of prey		
Source	d.f.	coefficient	*P*	d.f.	coefficient	*P*
Head depth	1, 231	0.129	0.0125*	1, 255	0.036	0.0079*
Head width	1, 232	−0.132	0.0066*	1, 257	−0.001	0.9537
Depth × width	1, 224	0.978	0.4549	1, 249	−0.265	0.3971

Note: Diet measurements and morphological traits are residuals after regression against the body size of the newt. Pond was entered in both models as a random effect; comparison with nested models not including pond revealed that the variance component due to pond was significant in both cases ($P < 0.001$). Denominator degrees of freedom (d.f.) for fixed effects are calculated using the Satterthwaite approximation (SAS Institute, 1999). Variables are measured in units of cm (newt morphology), mm (prey width), or mm^3 (prey volume). Asterisks indicate statistical significance (at $\alpha = 0.05$). Individuals that ate relatively large prey had deep and narrow heads, while those that consumed large quantities of prey had deep heads.

has been shown to induce variation in trophic morphology (Pfennig, 1990; Walls *et al.*, 1993; Loeb *et al.*, 1994; Michimae and Wakahara, 2002).

Developmental plasticity in head shape was also induced by predatory dragonfly larvae (Fig. 2), and here the response was focused on head depth, the structure most closely correlated with diet in the field (Fig. 1). The mechanism by which predators induce plasticity in head shape is unknown, but the results of our experiment rule out the possibility

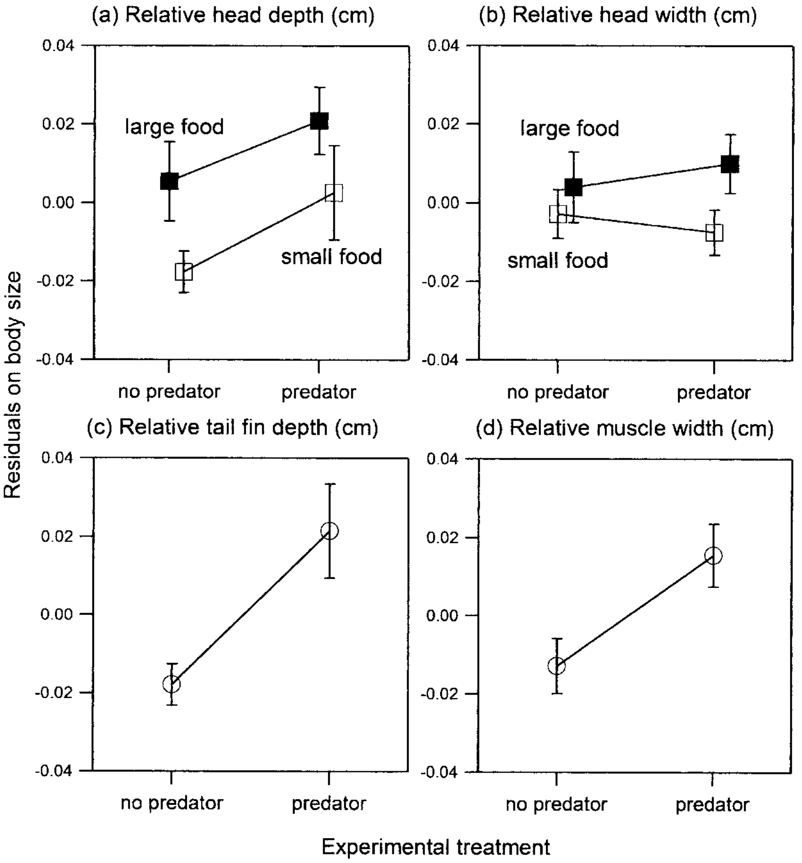

Fig. 2. Effects of experimental manipulation of predator presence and food size on the morphology of newt larvae. The upper panels (a, b) show the effects of predator and food size treatments on head shape. The lower panels (c, d) show the effects of predator treatment on the tail; these traits were not influenced by food size. Values (means ± standard errors) are residuals from a regression of morphological traits on overall body size and experiment. Higher values indicate deeper or wider traits.

that they first induce a shift in diet which then affects the head (Andersson, 2003; Eklöv and Svanbäck, 2006). Instead, a cue associated with dragonfly larvae causes *T. alpestris* larvae to develop relatively deep heads. It is therefore plausible that the deep head is an adaptation to risky environments, even though it has no impact on vulnerability to hunting predators (Van Buskirk and Schmidt, 2000).

The key to understanding the adaptive value of the head response lies in the relationship between head shape and foraging. Naturally occurring newt larvae with the predator-induced head shape captured larger prey items and had greater volumes of food in their stomachs. This means that newt larvae with deep heads enjoyed higher foraging success, because larger prey are known to be more profitable (Ranta and Nuutinen, 1985). Thus, the relatively large head may enable a newt to compensate for costs of mounting anti-predator defences. Costly defences include spending time hiding instead of feeding, and increasing

Table 2. Multivariate analyses of plasticity in head shape and tail shape in *Triturus alpestris* larvae in response to variation in predator presence and food size

Source of variation	d.f.	Wilks' *F*	*P*	Coefficients of the dominant eigenvector		
Head morphology				Head depth	Head width	
Body size	2, 37	4.92	0.0128	−0.67	8.85*	
Experiment	2, 37	10.78	0.0002	−2.04	9.45*	
Predator	2, 37	2.10	0.1363	6.10*	−2.05	
Food	2, 37	4.30	0.0209	3.23*	4.89*	
Predator × food	2, 37	0.58	0.5662	−4.54	9.19	
Tail morphology				Tail length	Tail fin depth	Tail muscle width
Body size	3, 36	2.17	0.1088	2.31	0.67	2.48
Experiment	3, 36	4.84	0.0062	2.36*	1.22*	1.73*
Predator	3, 36	3.99	0.0149	1.00	3.24*	0.75*
Food	3, 36	0.68	0.5716	0.74	−2.47	6.17
Predator × food	3, 36	0.80	0.5007	2.96	−0.98	2.38

Note: Asterisks indicate statistical significance in univariate analyses of variance (at $\alpha = 0.05$). The analysis includes the 44 larvae that survived to the end of the experiment.

investment to muscle and tail tissue. Although fitness costs have never been assigned to particular defensive traits in amphibians, the cost of the overall response has been measured repeatedly (Van Buskirk, 2000). Newt larvae may minimize this cost by immediately developing larger heads when they detect predation risk.

The possibility that larvae with large heads compensate for reduced foraging opportunity is supported by a field experiment on *Hynobius* salamanders (Kohmatsu *et al.*, 2001). In that study, larval growth rate was positively correlated with head width during the early and middle stages of development, but not late in development when all individuals were large. Although we could not perform a similar test in our experiment because larvae were fed *ad libitum*, our field data and these results from other salamanders suggest that larvae with predator-induced heads may experience higher growth rates due to their enhanced foraging success.

The predator-induced trophic response in newt larvae has an opposite effect on feeding from the response observed in frog larvae. While newts exposed to dragonflies develop larger mouths, associated with consuming more, larger, and more profitable prey (Fig. 1) (Ranta and Nuutinen, 1985), anuran tadpoles develop smaller mouths and tooth rows (Relyea and Auld, 2005). If anything, the anuran response would reduce foraging success. These divergent trophic responses may help to explain why predators cause consistent reductions in the growth rate of anuran larvae (Van Buskirk, 2000) but variable changes in the growth of *Triturus* larvae (Schmidt and Van Buskirk, 2005). Thus, while predator-induced plasticity in trophic morphology may be a general phenomenon (Relyea and Auld, 2005), its consequences could vary among taxa.

The deep head does not entirely eliminate the problem of costs for newts, but instead transfers the issue to another structure. If the head compensates for growth costs of responding to predators through enhanced feeding performance, there must be reasons why foraging efficiency is not always enhanced and why head shape is developmentally plastic. It could be that trophic morphology and foraging efficiency are under selection mostly when exposed to harsh conditions (Illius *et al.*, 1995), such as when predators are abundant.

Alternatively, a large head may enable growth rate to be higher than optimal when predators are absent, resulting in well-known costs of rapid growth (Arendt *et al.*, 2001; Munch and Conover, 2004). This argument suggests that costs associated with the large head are most pronounced in a predator-free environment, while the benefits of a deep head outweigh the costs when predators are present and foraging opportunities are more restricted.

Victims of natural enemies usually deploy multiple defences, and therefore endure multiple sources of costs (Benard, 2004). Most studies of inducible defences estimate the overall costs of defensive phenotypes without regard to particular traits, or simply assume that costs arise from single traits (in the case of amphibians, usually reduced foraging activity). However, to understand whole-organism function and to develop a reasonably complete model of phenotypic evolution, it is necessary to dissect behavioural, physiological, and morphological modes of response (Arnold, 1983, 2003). Such an approach will also be required to detect mechanisms by which costs associated with one mode of response are offset by shifts in other parts of the phenotype, and may reveal that compensatory mechanisms such as the one described here are widespread.

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