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Abstract

Phenotypic plasticity has important ecological consequences because the strengths of species interactions can change with the behavior and morphology of interacting individuals. Evolutionary studies of plasticity can predict conditions under which shifts in phenotypes will occur and, therefore, may modify species interactions. We studied evolutionary mechanisms maintaining an induced response to predators in Triturus newt larvae, which are among many taxa in freshwater habitats exhibiting predator-induced plasticity. When exposed to caged (nonlethal) Aeshna dragonfly larvae, newts of two species (T. alpestris and T. helveticus) spent more time hiding in the leaf litter, had darker pigmentation in the tail fin, and developed larger heads and larger tails relative to their body size, in comparison with newts in predator-free ponds. The two phenotypes faced a performance trade-off across environments with and without odonates: the predator-induced phenotype survived twice as well as the no-predator phenotype when exposed to free dragonflies, but the predator-induced phenotype of both species grew more slowly until just before metamorphosis. For Triturus alpestris, a direct comparison of performance between phenotypes was complicated because predator-induced newts emerged later in the summer but at a larger body size. Nonrandom mortality imposed by hunting dragonflies caused selection favoring increasing tail size, but we found no selection on specific traits in predator-free ponds. Head shape was not subject to selection in either environment; we suspect that head shape is involved in consuming different prey in the presence and absence of predators and is unrelated to predator escape. Triturus in 25 natural populations from which we collected quantitative samples in 1997 and 1998 exhibited extreme spatial variation in predation regime (density of large predators ranged from 0 to 24 individuals/m2). Variation among populations in head shape was exactly as predicted by experimental results (Triturus of both species had relatively large heads when exposed to predators), but results for tail shape were consistent with the experiments in only one of the two years. The evolutionary mechanisms maintaining plasticity in Triturus and other amphibian larvae should apply to many organisms inhabiting freshwater ponds, so trait-mediated indirect effects seem especially likely to occur in these habitats.

PREDATOR-INDUCED PHENOTYPIC PLASTICITY IN LARVAL NEWTS: TRADE-OFFS, SELECTION, AND VARIATION IN NATURE

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Abstract. Phenotypic plasticity has important ecological consequences because the strengths of species interactions can change with the behavior and morphology of interacting individuals. Evolutionary studies of plasticity can predict conditions under which shifts in phenotypes will occur and, therefore, may modify species interactions. We studied evolutionary mechanisms maintaining an induced response to predators in *Triturus* newt larvae, which are among many taxa in freshwater habitats exhibiting predator-induced plasticity. When exposed to caged (nonlethal) *Aeshna* dragonfly larvae, newts of two species (*T. alpestris* and *T. helveticus*) spent more time hiding in the leaf litter, had darker pigmentation in the tail fin, and developed larger heads and larger tails relative to their body size, in comparison with newts in predator-free ponds. The two phenotypes faced a performance trade-off across environments with and without odonates: the predator-induced phenotype survived twice as well as the no-predator phenotype when exposed to free dragonflies, but the predator-induced phenotype of both species grew more slowly until just before metamorphosis. For *Triturus alpestris,* a direct comparison of performance between phenotypes was complicated because predator-induced newts emerged later in the summer but at a larger body size. Nonrandom mortality imposed by hunting dragonflies caused selection favoring increasing tail size, but we found no selection on specific traits in predator-free ponds. Head shape was not subject to selection in either environment; we suspect that head shape is involved in consuming different prey in the presence and absence of predators and is unrelated to predator escape. *Triturus* in 25 natural populations from which we collected quantitative samples in 1997 and 1998 exhibited extreme spatial variation in predation regime (density of large predators ranged from 0 to 24 individuals/m^2). Variation among populations in head shape was exactly as predicted by experimental results (*Triturus* of both species had relatively large heads when exposed to predators), but results for tail shape were consistent with the experiments in only one of the two years. The evolutionary mechanisms maintaining plasticity in *Triturus* and other amphibian larvae should apply to many organisms inhabiting freshwater ponds, so trait-mediated indirect effects seem especially likely to occur in these habitats.

Key words: Aeshna; *induced defense; natural selection; newt larvae; phenotypic plasticity; predation risk; Switzerland;* Triturus.

INTRODUCTION

The process of generalizing across systems represents an important challenge in ecology. If the strengths of species interactions change with the context in which they occur, then how can the results of any specific study be applicable in broader context? Proposed solutions to this question generally emphasize the dialogue between theory, functional and mechanistic understanding, and field studies (Tilman 1987, Wainwright 1996, Werner 1998). Here we argue that a focus on the evolutionary maintenance of phenotypic design represents another solution to this question, because traits are intimately involved in species interactions, and information on the evolutionary basis of traits can inform predictions about their occur-

rence in novel systems. We offer an example in which understanding how selection maintains phenotypic plasticity leads to general predictions about changing interaction strengths in aquatic communities.

Many aspects of the phenotype are functionally connected with ecological performance and therefore may be maintained by selection associated with species interactions (MacArthur 1972, Abrams 1996, Schluter 1996). Thus, phenotypic design may reflect the dominant interactions that influence an organism's performance. Comparisons among species indicate that the importance of competition and predation vary with morphological and behavioral traits. For example, species of plants and animals that are effective at competition and occur within communities where competition is pervasive tend to possess well-developed suites of traits involved in exploiting resources (Tilman and Wedin 1991, Ryser and Lambers 1995, Smith and Van Buskirk 1995, Biere 1996). Experiments on phenotyp-

ically plastic species likewise suggest that the strengths of dominant interactions change as phenotypes shift within species (Wissinger and McGrady 1993, McCollum and Van Buskirk 1996, Werner and Anholt 1996, Peacor and Werner 1997). For example, anuran larvae that alter behavior and morphology to minimize their mortality risk from predation impose a reduced competitive impact on other species (Werner and Anholt 1996, Peacor and Werner 2000). Thus, attention to the phenotype may provide mechanistic insight into interaction strengths within communities.

Predicting changes in species interactions caused by phenotypic plasticity is a challenging problem in community ecology, but one for which an evolutionary perspective may prove useful. An extensive theoretical literature identifies conditions under which plasticity is likely to evolve (Via and Lande 1985, Van Tienderen 1991, Gomulkiewicz and Kirkpatrick 1992, De Jong 1995), and numerous empirical studies address the fitness costs and benefits of alternative phenotypes (Karban and Baldwin 1997, Tollrian and Harvell 1999). These evolutionary studies provide a strong basis for predicting the occurrence of plasticity and for anticipating when it might alter species interactions. Here we take an evolutionary approach in a study of predator-induced plasticity in newt larvae (Salamandridae: *Triturus*). Our work shows how selection favors plasticity, and suggests that plasticity may influence species interactions by changing individual growth rates and vulnerability to predators. Conditions within freshwater ponds are favorable for the evolution of predator-induced responses, and our results combine with many other studies to demonstrate that induced defenses are widespread in these habitats and trait-mediated changes in species interactions are likely. Although the emphasis here is on measuring phenotypic variation and estimating its fitness effects, we hope to show that an evolutionary approach to traits that are involved in species interactions can offer general insight that will be of use to ecologists.

Amphibian larvae are good model organisms for studying the relationship between individual traits and ecological performance. Comparisons among species suggest that particular phenotypes are associated with enhanced competitive ability or predator escape. For example, species with relatively active foraging behavior often exhibit high individual growth rate but increased vulnerability to predators (Lawler 1989, Werner 1992, Skelly 1995, Smith and Van Buskirk 1995). Comparisons of phenotypically different individuals within species confirm that behavioral and morphological variation can affect mortality rates or competitive effects, thus potentially altering species interactions (Anholt and Werner 1995, McCollum and Van Buskirk 1996, Werner and Anholt 1996). Demonstrations of natural selection acting on these same traits shed light on the evolutionary maintenance of plasticity and phenotypic differences between species (Van Buskirk et al. 1997, Van Buskirk and Relyea 1998), and therefore lay out a general picture of when we should expect to

find plasticity that may quantitatively alter species interactions.

One way to assess the generality of the anuran results is to move to a new system, but one that shares important features with the anuran system. Predator-induced morphological plasticity has not previously been described in salamanders, and the relationships of morphology and behavior to performance are less well known than in tadpoles. Nevertheless, the larvae of *Triturus* newts occupy habitats similar to those of tadpoles (the two taxa often co-occur and share the same predators), and their habitat fulfills most conditions thought to be necessary for the evolution of plasticity (Dodson 1989). *Triturus* occur in ponds, where water can effectively transmit the chemical signals that contain information about environmental conditions such as the presence of predators. Although salamander larvae are ecologically different from anuran larvae (i.e., predators rather than herbivores), their individual fitness is probably affected by variation in predator presence, as is the case for anurans (Smith 1983, Woodward 1983, Van Buskirk et al. 1997). Finally, exposure of newt larvae to predators is potentially variable in natural populations. The predator composition of ponds can change from one year to the next (Jefferies 1994, Van Buskirk and Relyea 1998), and *Triturus* have a terrestrial adult stage during which some dispersal among ponds with differing predation regimes may take place (Griffiths 1996, Joly and Grolet 1996, Kupfer 1998, Baker and Halliday 1999). These conditions lead us to expect that larval newts will exhibit plasticity in response to predators much like that found in tadpoles, and that plastic responses will decrease vulnerability to predation.

The goals of our study were to measure behavioral and morphological plasticity in larvae of the two most common and widespread newts in northern Switzerland, *Triturus alpestris* (alpine newt) and *T. helveticus* (palmate newt; Grossenbacher 1988), and to determine whether plasticity is maintained by divergent selection across environments similar to that found in anuran larvae. We began by measuring the extent of plasticity in newts experimentally exposed to the presence or absence of nonlethal dragonfly larvae. Next, we performed a short-term predation trial with *T. helveticus* to estimate the consequences of phenotypic shifts for the interaction between newts and dragonflies. Differential mortality in the predation trial and differential growth in the absence of predators provided measures of how natural selection maintains plasticity. We continued the plasticity experiment on *T. alpestris* through metamorphosis to assess the impact of predators on life history traits. Finally, we surveyed a number of ponds in the field to ask whether natural phenotypic variation is related to the occurrence of predators and can be predicted from experimental estimates of selection and plasticity.

METHODS

Plasticity experiments

We measured phenotypic plasticity of two *Triturus* species by rearing them through most of the larval stage

in outdoor artificial ponds in the presence or absence of predatory dragonfly larvae. The ponds were fiberglass stock tanks, placed in a field on the campus of the University of Zürich, Switzerland, and filled to a depth of 40 cm (1.35 m² surface area, 550 L volume). Tightly fitting lids, constructed of 35% shade cloth, prevented colonization by unwanted insects and amphibians. We manipulated the predator composition of the tanks by enclosing three late-instar *Aeshna cyanea* inside floating cages within half the tanks. The cages were constructed of a 10 cm length of plastic tube (12 cm diameter), capped at both ends with fiberglass window screen. Three empty cages floated in the no-predator tanks. Every other day throughout the experiment, the dragonflies were fed 300 mg of a mixture of *Triturus* larvae and *Rana temporaria* or *R. ridibunda* tadpoles. The two treatments were replicated four times in a completely randomized design.

Within the tanks we established aquatic communities typical of ponds in the surrounding area. The tanks were filled with tap water on 6 March 1997 for the *T. helveticus* experiment, and on 7 March 1998 for the *T. alpestris* experiment. Over the following week we added 0.5 kg dried leaf litter, 10 g commercial rabbit food, and three separate inoculations of water and zooplankton collected from nearby ponds. These ingredients created structural heterogeneity covering the bottoms of the tanks and provided a nutrient base for a diverse community of microbes and microinvertebrates. We also added several adult snails (*Lymnaea stagnalis*; six in 1997 and three in 1998) to control periphyton growth and promote nutrient cycling.

The plasticity experiments began on 4 June 1997 (*T. helveticus*) and 10 May 1998 (*T. alpestris*), when we added 15 larvae of the appropriate species to each tank. The newts were hatched from eggs laid in captivity by adults collected near Basel (*T. helveticus*) and Zürich (*T. alpestris*), Switzerland; they were ~1–2 weeks old and weighed 6.9 ± 3.0 mg (mean ± 1 SD for *T. helveticus*) and 12.8 ± 2.5 mg (*T. alpestris*) when the experiment began. Larvae from ~12 female *T. helveticus* and ~20 female *T. alpestris* were used in the experiments. The timing of the two experiments differed not because of species differences in timing of reproduction (Griffiths 1996), but because oviposition occurred earlier during the second year.

The goal of these experiments was to record the behavior, morphology, and life history of newt larvae in ponds with dragonflies and with no predators. To measure activity we conducted counts of the number of larvae visible on or above the leaf litter in each tank on several occasions, continuing until just before metamorphosis began. On one sample of the *T. helveticus* experiment we checked the tanks in both day and night; the same number of newts was seen in each treatment on both censuses, so we performed all subsequent samples during the day.

The *T. helveticus* experiment was halted when the tanks were drained on 17 July 1997 (day 43), and all survivors were counted and weighed. A sample of eight larvae was made from the *T. alpestris* experiment at about the same time (day 40), for comparison of growth rates. For both species this sample occurred just as the first metamorphs appeared, when most individuals exhibited the maximal development of their gills (stage 54 of Gallien and Bidaud 1959). The *T. alpestris* experiment was continued until metamorphosis was complete; we continued to feed the predators on schedule and check for metamorphs every day until the tanks were drained on 2 September 1998. At that point only a single individual remained in the water, and even it had nearly lost its gills.

We sampled newt morphology on three occasions: on the first day of the experiment, about halfway through the larval period, and just before metamorphosis. For the initial sample we preserved 10 randomly chosen hatchlings in 10% formalin. For the halfway sample we captured five (*T. helveticus*) or eight (*T. alpestris*) newts from each tank using a small dipnet, photographed them, and returned them immediately to the experiment. For the final sample we measured every surviving individual (*T. helveticus*) or a sample of eight individuals which were again returned (*T. alpestris*). Newts were placed within a small water-filled plexiglass chamber and photographed using a 35-mm camera equipped with a 50-mm macro lens. The chamber was fitted with mirrors that gave simultaneous side- and bottom-view images on the same negative. We digitized the three-dimensional coordinates of 31 landmarks directly from the negative projected onto a computer video monitor via a digital camera. The landmarks were situated to identify size and shape (i.e., tip of tail, base of legs, tip of snout), and to enable us to measure traits expected to be functionally important (i.e., tail length and depth, head width). Fig. 1 depicts projections of landmarks onto two-dimensional planes (See the Appendix for a complete map of the landmarks).

Our morphometric analyses focused on eight size-corrected linear distances between pairs of landmarks. The distances were the residuals after regression against overall body size, which was calculated as the square root of the centroid size (i.e., the sum of the squared distances among all pairs of landmarks; Bookstein 1991). The linear distances, depicted in Fig. 1, were head length from tip of snout to anterior edge of gills, maximum width and depth of the head at the gills, torso length from front legs to hind legs, tail length from hind legs to tail tip, and tail depth, tail muscle depth, and tail muscle width measured at one-third of the distance between the base and tip of the tail. For each trait we performed a single regression against size, including all individuals from both experiments. These regressions were highly significant (R^2 values were between 0.79 and 0.98 and averaged 0.87); transformation was unnecessary because the eight measurements were linearly related to the square root of centroid size.
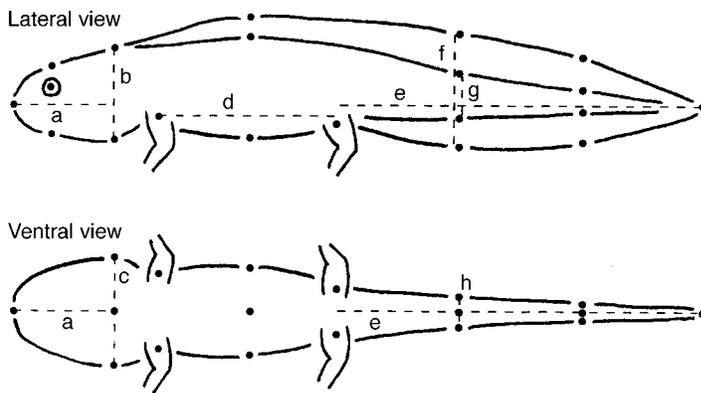
Fig. 1. Lateral and ventral projections of landmark locations on *Triturus* larvae reared in experiments and collected in the field samples. Lines represent the eight linear measures extracted from the landmark data: a, head length; b, head depth; c, head width; d, torso length; e, tail length; f, tail fin depth; g, tail muscle depth; h, tail muscle width.

An error in the photographic process caused a portion of the image to be blurred for 40 of the 91 *T. helveticus* sampled at the end of the experiment; these newts were discarded from analysis.

We estimated the extent of black color in the tail of every photographed newt larva using a gray-scale score provided by the image analysis software. Our measure of tail color was the mean gray-scale reading from four regions of the tail fin: within the distal 20% and the distal 20–40% of the tail and extending from just above or below the muscle to the edge of the fin. Gray-scale was measured relative to standard bright and dark objects that occurred within every image.

We tested the significance of plasticity by comparing the behavior, tail color, and morphology of newts in the presence and absence of caged dragonflies. We analyzed the results of both experiments simultaneously to provide insight into differences between *T. alpestris* and *T. helveticus,* although a ''species effect'' defined this way will include any other differences between experiments that affected the phenotype of larval newts. For morphology we used multivariate analyses of variance on each sample date, because phenotypic correlations among shape variables might cause the plastic response of a single multidimensional trait to show up in univariate tests as significant responses in several separate traits. The dominant eigenvector for the predator treatment effect in MANOVA represented the pattern of plasticity exhibited by all traits together, after accounting for correlations among traits. This vector is the linear combination of the response traits that distinguished most clearly between newts originating from the two environments; thus it defines the principal phenotypic axis along which plasticity was expressed (Littell et al. 1991). We also performed univariate repeated measures ANOVAs on the middle and final samples of refuge use, tail color, and morphology to illustrate how each variable responded to the difference between tank treatments when viewed in isolation.

Vulnerability to predation

We used a short-term predation experiment to evaluate whether phenotypic plasticity helps protect newts from predation. Survivors from the *T. helveticus* plasticity experiment were weighed and photographed, and those that showed no sign of approaching metamorphosis were employed in the predation trial (i.e., earlier than stage 55, Gallien and Bidaud 1959). Photographs provided a means of identifying individuals, based on unique arrangements of dark speckles and blotches on the sides and tail. The experiment took place outdoors in 12 plastic tubs containing 65 L water (0.28 m^2 surface area), 175 g leaf litter, and 150 g floating aquatic vegetation (*Myriophyllum*). Each tub received six newt larvae, three from the no-predator treatment and three from the caged-*Aeshna* treatment, chosen at random but preferably drawn from different tanks in the plasticity experiment. This design presented the predators with a choice between the two phenotypes. We placed one final-instar aeshnid dragonfly larva into each tub, using *Aeshna cyanea* in half the tubs and *Anax imperator* in the other half, because we had too few final-instar larvae to use only one species. *Aeshna* and *Anax* are approximately the same size (40–45 mm total body length in the final instar). The tubs did not contain food for the newt larvae, or alternate prey for the odonates.

The predation trial lasted for 2–6 d, the duration depending on the course of mortality over time within each tub. We checked all tubs after 2 and 4 days, and drained the tub and photographed all survivors when the dragonfly had killed at least two of the six newts. The trial did not last long enough for newts to develop morphological responses to predators.

Estimates of natural selection

We estimated phenotypic selection in two ways. First we asked whether the predator-induced and no-predator phenotypes survived or grew at different rates in the presence and absence of predators. This told us whether the entire suite of traits induced by the two environments (including behavior, morphology, and tail color) influenced predator escape and growth. Second, we estimated selection acting on specific morphological traits by testing whether surviving individuals in the predation trial were a nonrandom subset of the initial population with respect

to morphology, and by regressing growth against individual traits in the plasticity experiment.

We calculated the selection differential imposed by aeshnid dragonflies as the change in mean phenotype of *T. helveticus* within each tub during the course of the predation trial (mean trait value of survivors minus mean value of the six larvae prior to selection). Selection differentials were divided by the standard deviation of the trait in the population before selection to yield a measure of the relative intensity of selection (Falconer and Mackay 1996). The selection intensity for a particular trait was large if dragonflies killed newts nonrandomly with respect to that trait. As before, we analyzed the results using MANOVAs on head and tail traits, and inspected the dominant eigenvector to determine the primary axis of selection acting on groups of correlated traits. The Intercept term in the analysis tested for selection by determining whether the mean selection intensities (averaged across both predator species) differed from zero, and the Predator Species term asked whether selection intensities differed between tubs having *Aeshna* and *Anax*.

To check for selection in the absence of free predators we regressed individual mass just before metamorphosis against the eight morphological traits and the predator treatment. We did this only for *T. helveticus,* because we do not have individual data for the mass of *T. alpestris.* The treatment effect checked for an overall growth cost of mobilizing and possessing the phenotypic response to predators, whereas the effects of the separate traits tested whether individual growth rate within treatments varied with morphology. Our use of body mass at the end of the experiment as a correlate of fitness is justified by field studies showing that size at metamorphosis is related to adult survival and to size or timing of first reproduction in amphibians (Smith 1987, Semlitsch et al. 1988, Berven 1990, Scott 1994).

Field samples of predators and newt morphology

We made quantitative samples of predators and newt larvae in a series of ponds in Cantons Zürich and Thurgau, Switzerland, during July 1997 (24 ponds) and July 1998 (31 ponds). The purpose was to estimate the distribution of newt larvae with respect to predators, and to assess whether naturally occurring *Triturus* exhibit changes in morphology consistent with the experimental results. Most of our study ponds were probably created by human activities, but many are decades old. We made samples by rapidly plunging a pipe (100 cm long, 35 cm diameter, 0.096 m² surface area) into the substrate of the pond, and removing all captured amphibians and potentially predaceous animals (>4 mm total body length) using a small net. All predators were collected for later identification and measurement, except for adult newts, which were identified, measured, and released. We made 20–35 pipe samples in each pond, and ≤35 in larger ponds, except for ponds that were too small to accommodate 20 pipe throws. The

samples were distributed among habitat types within the pond according to the frequency of the habitats (within areas <1 m deep), but the exact location of each sample was chosen haphazardly. We also dipnetted for 15 min in each pond to sample rare taxa that were not caught in pipe samples.

The larvae of four *Triturus* species occur in our ponds, and two of them (*Triturus helveticus* and *T. vulgaris*) cannot be distinguished by external morphology (Arntzen et al. 1998). Our analyses of field-sampled newts therefore combine the results for *T. helveticus* and *T. vulgaris* into a single taxon. In 1997 we preserved in 10% formalin the first 20 newt larvae from the pipe samples in ponds with only one *Triturus* species present, and the first 30 larvae in ponds with more than one species. In 1998 we preserved the first 20 *T. alpestris* larvae, but made photographs of the first 20 *T. helveticus/vulgaris* while they were alive. Larvae of the fourth species, *T. cristatus,* were uncommon in our samples (0 ponds in 1997 and 3 ponds in 1998) and will not be discussed here. We digitized the locations of the same landmarks described above for all the field-sampled specimens with undamaged tails, 10–15 wk after preservation. During that period the preserved specimens probably underwent some formalin-induced shrinkage (Van Buskirk et al. 1997).

Analysis of the field samples tested for a relationship between newt morphology and predator abundance. Morphological variables were the same as in our experimental analyses. Predator abundance was defined as the combined density of aeshnid dragonfly larvae (*Anax* and *Aeshna*) and dytiscid beetle adults and larvae (mostly *Dytiscus, Cybister, Acilius,* and *Ilybius*). Other predators that occurred in the ponds were either very scarce or considerably less threatening to amphibian larvae (Smith 1983, Formanowicz 1986). These included libellulid dragonflies, hemipterans such as *Nepa* and *Notonecta, Sialis* (Megaloptera), leeches, larval hydrophylid beetles, and adult *Triturus.* We also restricted analysis to individual predators ≥15 mm in total body length, because smaller predators represent a limited mortality risk (Caldwell et al. 1980, Smith 1983, Wilbur 1984). The density of species that occurred only in the dipnet was set to one-half the lowest possible density in the pipe samples. As above, we used the dominant eigenvector from MANOVA to indicate which traits varied most strongly with predator density.

RESULTS

Life history responses to predators

Caged predators had no impact on the survival of newt larvae in either experiment (Table 1; $P > 0.6$ in both species, ANOVA).

The mean body mass of surviving larvae after six weeks, just before metamorphosis began, was smaller in the presence of dragonflies for both *Triturus* species. In *T. helveticus* the reduction in mass due to predators

TABLE 1. Larval performance of *Triturus alpestris* and *T. helveticus* in the presence and absence of caged *Aeshna* dragonflies.

		Response					
Species	Treatment	Survival to meta-morphosis	Survival to week 6	Mass at week 6 (mg)	Growth to week 6 (%/d)	Mass at meta-morphosis (mg)	Age at meta-morphosis (d)
Triturus alpestris	No predator	0.83 (0.08)	...	481.3 (10.5)	9.74 (0.06)	389.3 (6.79)	68.7 (0.8)
	Caged-*Aeshna*	0.77 (0.10)	...	434.9 (21.5)	9.45 (0.14)	439.0 (9.57)	84.4 (2.4)
Triturus helveticus	No predator	...	0.83 (0.06)	258.4 (11.9)	8.78 (0.12)	...	...
	Caged-*Aeshna*	...	0.80 (0.11)	201.0 (5.6)	8.15 (0.07)	...	...

Notes: The two experiments lasted for different durations, and therefore not all responses were measured for both species. Entries in the table show the mean, followed by 1 SE in parentheses.

was 22%; in *T. alpestris* the reduction was only 9.6%. *Triturus alpestris* was larger than *T. helveticus* throughout the experiment, but its initial size advantage at hatching did not fully explain its larger size after six wk: daily growth rate, assuming an exponential growth model, was 13% larger for *T. alpestris* than for *T. helveticus* (Table 1; species effect in ANOVA on growth rate: $F_{1,12} = 124.0$, $P = 0.0001$) and significantly reduced in the caged-*Aeshna* treatment (3% reduction for *T. alpestris,* 7% reduction for *T. helveticus*; predator effect: $F_{1,12} = 20.6$, $P = 0.0007$; interaction not significant). Newts exposed to *Aeshna* showed reduced size throughout the experiment, as reflected by the significant predator effect in repeated measures analysis of centroid size (Table 2). Taken together, these results point to a growth cost of the phenotypic response to predators, especially in *T. helveticus,* but no survival cost. Newts in the caged-*Aeshna* ponds detected predators and responded to them even though no actual risk of predation existed, and as a result they grew more slowly during their first six wk.

The results for size and age at metamorphosis in *T. alpestris* make the growth cost of responding to predators less clear (Table 1, Fig. 2). Newts metamorphosed about 16 d later in ponds with predators ($F_{1,6} = 62.1$, $P = 0.004$), but they also emerged at a 13% larger size on average ($F_{1,6} = 30.1$, $P = 0.012$). Covariance analysis indicated that the treatment effect on body size was entirely an outcome of later metamorphosis when predators were present: after correcting for the relationship between mass and date of emergence, there was no residual effect of predator treatment on size at metamorphosis (Fig. 2). Thus, *T. alpestris* larvae initially grew slowly when they detected predators, but they eventually recovered that deficit and emerged later and larger than larvae in the absence of predators. We cannot assess the net effect of these shifts without knowing how fitness varies with simultaneous changes in body size and date of metamorphosis (e.g., McPeek and Peckarsky 1998).

Plasticity in behavior, color, and morphology

The two *Triturus* species both showed strong phenotypic plasticity in response to the predator treatment. Early in development newts spent most of the time hiding in all tanks, but after about three weeks there

TABLE 2. Repeated-measures analyses of phenotypic plasticity in *Triturus alpestris* and *T. helveticus* larvae exposed to environments having either caged *Aeshna* larvae or no predators.

	Source of variation					
Response	Date	Species	Predator	Date × species	Date × predator	Species × predator
Refuge use	19.66 (0.0002)*	28.61 (0.0002)*	40.78 (0.0001)*	4.51 (0.0371)*	4.51 (0.0370)*	0.01 (0.9149)
Tail color	1.13 (0.3096)	44.71 (0.0001)*	19.58 (0.0008)*	16.58 (0.0015)*	5.38 (0.0388)*	5.08 (0.0437)*
Body size	2266.43 (0.0001)*	110.30 (0.0001)*	10.58 (0.0069)*	106.06 (0.0001)*	6.08 (0.7883)	1.55 (0.2370)
Relative head length	0.44 (0.5215)	3.19 (0.0991)	4.56 (0.0540)	0.03 (0.8622)	0.58 (0.4597)	1.84 (0.1995)
Relative head depth	2.41 (0.1461)	56.84 (0.0001)*	2.56 (0.1357)	0.24 (0.6350)	10.93 (0.0063)*	0.02 (0.8837)
Relative head width	2.18 (0.1659)	102.93 (0.0001)*	18.99 (0.0009)*	4.46 (0.0563)	1.57 (0.2343)	0.01 (0.9272)
Relative torso length	16.29 (0.0017)*	10.83 (0.0065)*	5.35 (0.0392)*	0.04 (0.8491)	3.28 (0.0954)	3.85 (0.0734)
Relative tail length	11.88 (0.0048)*	30.40 (0.0001)*	3.08 (0.1049)	0.03 (0.8735)	4.59 (0.0535)	6.77 (0.0231)*
Relative tail fin depth	5.86 (0.0322)*	20,80 (0.0007)*	33.52 (0.0001)*	0.82 (0.3817)	4.14 (0.0646)	0.57 (0.4642)
Relative tail muscle depth	30.55 (0.0001)*	33.08 (0.0001)*	0.00 (0.9977)	0.52 (0.4858)	6.40 (0.0264)*	2.67 (0.1280)
Relative tail muscle width	0.26 (0.6210)	18.09 (0.0011)*	13.78 (0.0030)*	0.98 (0.3425)	4.03 (0.0678)	0.06 (0.8070)

Notes: The data come from separate experiments performed on the two species, so effects involving species may be confounded with other differences between experiments. Refuge use is the proportion hiding. Tail color is a gray-scale measurement of the terminal 40% of the tail fin. Body size is the square root of centroid size, and morphological traits are calculated relative to body size. Refuge use was scored on three dates; other traits were measured halfway through the larval period and just before metamorphosis. Entries in the table are *F* values, followed by the *P* value in parentheses. The degrees of freedom for all tests are 1, 12 except for date and its interactions for refuge use, for which the degrees of freedom are 2, 11.
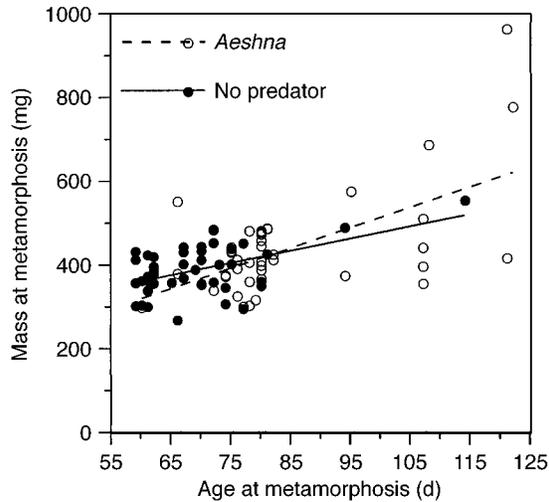
* $P < 0.05$.

FIG. 2. Size and age at metamorphosis of *Triturus alpestris* reared in the presence and absence of caged dragonfly larvae. The experiment began on 10 May, when newts were ~7 d old, and metamorphosis extended from 1 July until 2 September. There was a size increase with date in both treatments, and no overall effect of treatment (a model assuming linear increase in mass with date provided the best fit: predator, $F_{1,85} = 2.02$, $P = 0.1585$; date, $F_{1,85} = 30.4$, $P = 0.0001$; date × predator interaction, $F_{1,85} = 1.90$, $P = 0.1714$).

were typically 2–4 individuals openly visible in the predator-free tanks (Fig. 3). When dragonflies were present *T. helveticus* was never found in the open, whereas *T. alpestris* was observed in small numbers.

The species and predator effects on refuge use were highly significant in repeated measures analysis, indicating that *T. alpestris* hid less often than *T. helveticus* and that caged *Aeshna* caused a reduction in the number visible (Table 2). The absence of a species-by-predator interaction indicates that both species increased refuge use by about the same amount when they detected predators. Because ~80% of the newts survived in both experiments and in both predator treatments (Table 1), and because the two species did not differ in visibility, differences in the number of visible larvae reflect real behavioral responses to predation and differences between species.

Both species developed darker tail fins when predators were present, and the response to predators increased significantly with time (Fig. 4, Table 2). The tail of *T. alpestris* was darker than that of *T. helveticus* under most conditions, but this was especially true in the caged-*Aeshna* treatment and late in the experiment (Table 2).

Strong phenotypic correlations among some of the eight morphological traits illustrated that these characters were not independent, and supported our decision to focus on multivariate analyses of shape (Table 3). For example, relative torso length was negatively correlated with head length and tail length in both environments, presumably because the relative positions of the legs was variable. There was no tendency for the four tail traits to be positively correlated with one another, as expected under a hypothesis of tight functional integration (Cheverud 1996); tail traits were not
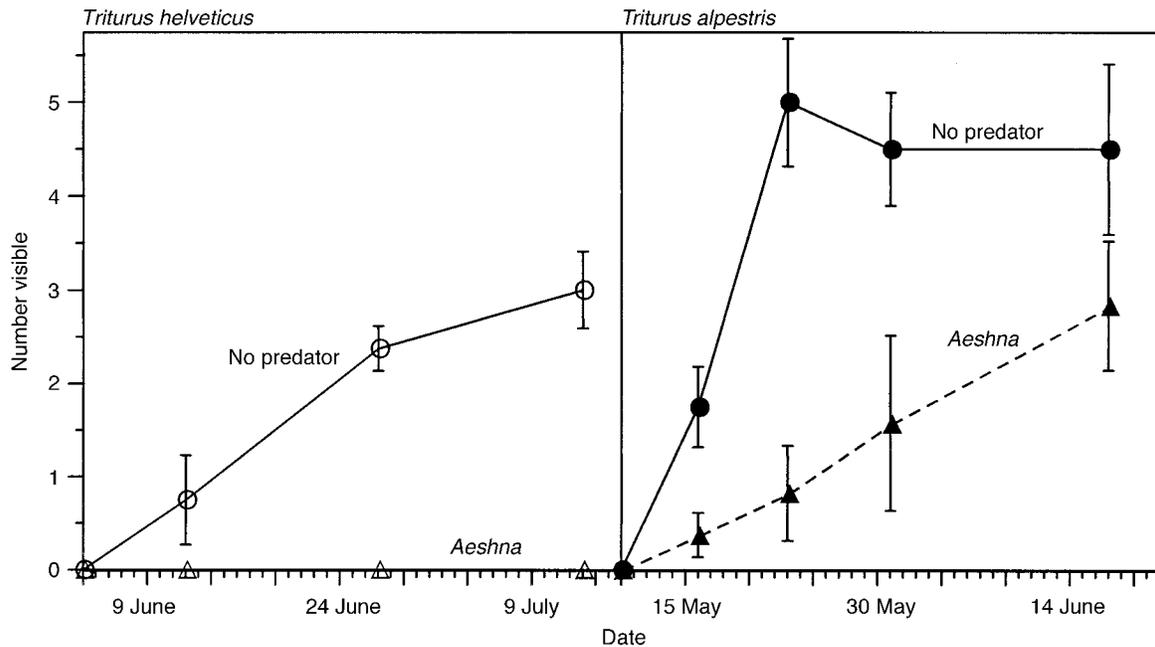

FIG. 3. Number of newt larvae visible in the artificial ponds on daytime censuses extending from shortly after hatching until just before metamorphosis. Error bars depict ± 1 SE of the mean. *Triturus alpestris* was more active than *T. helveticus,* and both species hid in the benthic litter more often when caged predators were present.
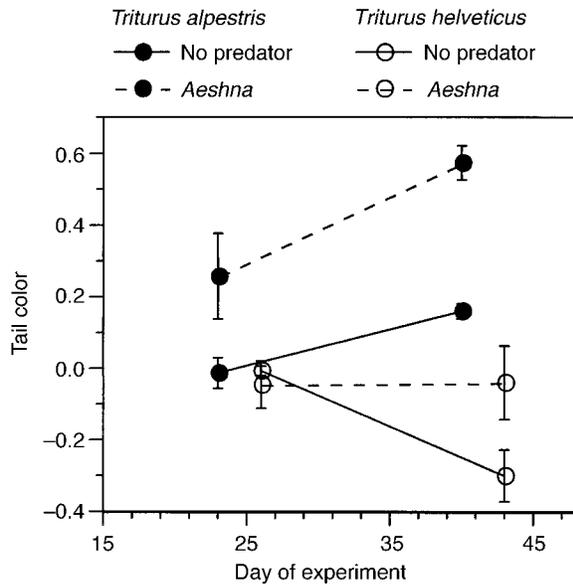
FIG. 4. Tail color of *Triturus alpestris* and *T. helveticus* larvae in the presence (dashed lines) and absence (solid lines) of caged *Aeshna* dragonfly larvae. Tail color is a mean gray-scale score for the terminal 40% of the tail fin; units are arbitrarily defined relative to standard light and dark objects that appeared within every photograph. Error bars depict ± 1 SE of the mean. *Triturus alpestris* had a darker tail fin than *T. helveticus,* and both species developed darker tails when exposed to dragonflies.

generally negatively correlated with head traits, as occurs in anuran larvae (Van Buskirk and Relyea 1998). The overall patterns of phenotypic correlation within the no-predator and caged-*Aeshna* environments were highly congruent (between treatment comparison for *T. alpestris*: $P = 0.0000$; *T. helveticus*: $P = 0.0001$; Mantel test, 10 000 randomizations, Mantel 1967). None of the shape variables was correlated with body size, as expected since we define shape in terms of residuals after regression on size.

Triturus alpestris larvae were larger and more robust than *T. helveticus* larvae (Fig. 5). Regardless of treatment, *T. alpestris* had a relatively wide and deep head, long torso, and short tail throughout development. Late in the larval period, *T. alpestris* also developed a deeper tail and larger tail muscle. The interspecific differences were significant in multivariate analyses for both sampling dates (Table 4) and in repeated measures analyses of the separate traits (Table 2).

Morphological responses to predators were evident in both species, and were stronger in the middle of the larval period than at the end of the experiment. We judge the intermediate sample to be somewhat more reliable because it was unaffected by photographic mishaps and morphological changes just prior to metamorphosis. Plasticity involved both head shape and tail shape (Tables 2 and 4). Large positive coefficients for head width and tail fin depth of the dominant eigenvector from MANOVA on the intermediate sample, and negative coefficients for torso length and tail length, indicated that newts became relatively short with wider heads and deeper tail fins when *Aeshna* was present. This interpretation was strengthened by repeated mea-

TABLE 3. Phenotypic correlations among morphological traits of individual *Triturus alpestris* and *T. helveticus* larvae sampled from the experimental ponds about halfway through the larval period.

Trait	Head length	Head width	Head depth	Torso length	Tail length	Tail fin depth	Tail muscle width	Tail muscle depth
A) *Triturus alpestris* (n = 32)								
Head length	⋯	0.579*†	0.737*†	0.126	−0.355*	0.073	0.006	0.012
Head width	0.280	⋯	0.561*†	0.206	−0.292	0.223	0.296	−0.018
Head depth	0.216	0.358*	⋯	−0.086	−0.102	0.159	0.130	0.166
Torso length	−0.096	−0.202	−0.160	⋯	−0.906*†	−0.159	0.210	0.094
Tail length	−0.230	0.128	0.105	−0.854*†	⋯	0.217	−0.076	−0.054
Tail fin depth	0.081	−0.025	0.058	−0.145	0.011	⋯	0.579*†	0.057
Tail muscle width	−0.122	0.201	−0.131	0.001	0.150	0.491*	⋯	0.137
Tail muscle depth	0.391*	−0.157	−0.132	0.057	−0.231	−0.329	−0.294	⋯
B) *Triturus helveticus* (n = 20)								
Head length	⋯	0.133	0.655*†	−0.566*	0.332	−0.047	0.073	0.218
Head width	0.333	⋯	−0.174	0.196	−0.321	0.302	0.099	−0.313
Head depth	0.647*	0.263	⋯	−0.695*†	0.574*	0.121	0.040	0.313
Torso length	−0.638*	−0.350	−0.795*†	⋯	−0.935†	−0.117	−0.078	−0.285
Tail length	0.538*	0.210	0.762*†	−0.896*†	⋯	0.040	−0.098	0.330
Tail fin depth	0.327	0.045	0.113	0.009	0.002	⋯	0.530*	−0.187
Tail muscle width	0.259	0.057	−0.113	0.070	−0.045	0.682*†	⋯	0.074
Tail muscle depth	0.502*	0.144	0.463*	−0.327	0.266	0.337	−0.142	⋯

Notes: Entries above the diagonal are correlation coefficients within the no-predator treatment; entries below the diagonal are from the *Aeshna* treatment. All traits are residuals after regression on body size, which is the square root of centroid size.

* $P < 0.05$.

† Significant after Bonferroni adjustment for $\alpha = 0.05$ across 28 tests ($P = 0.0018$).
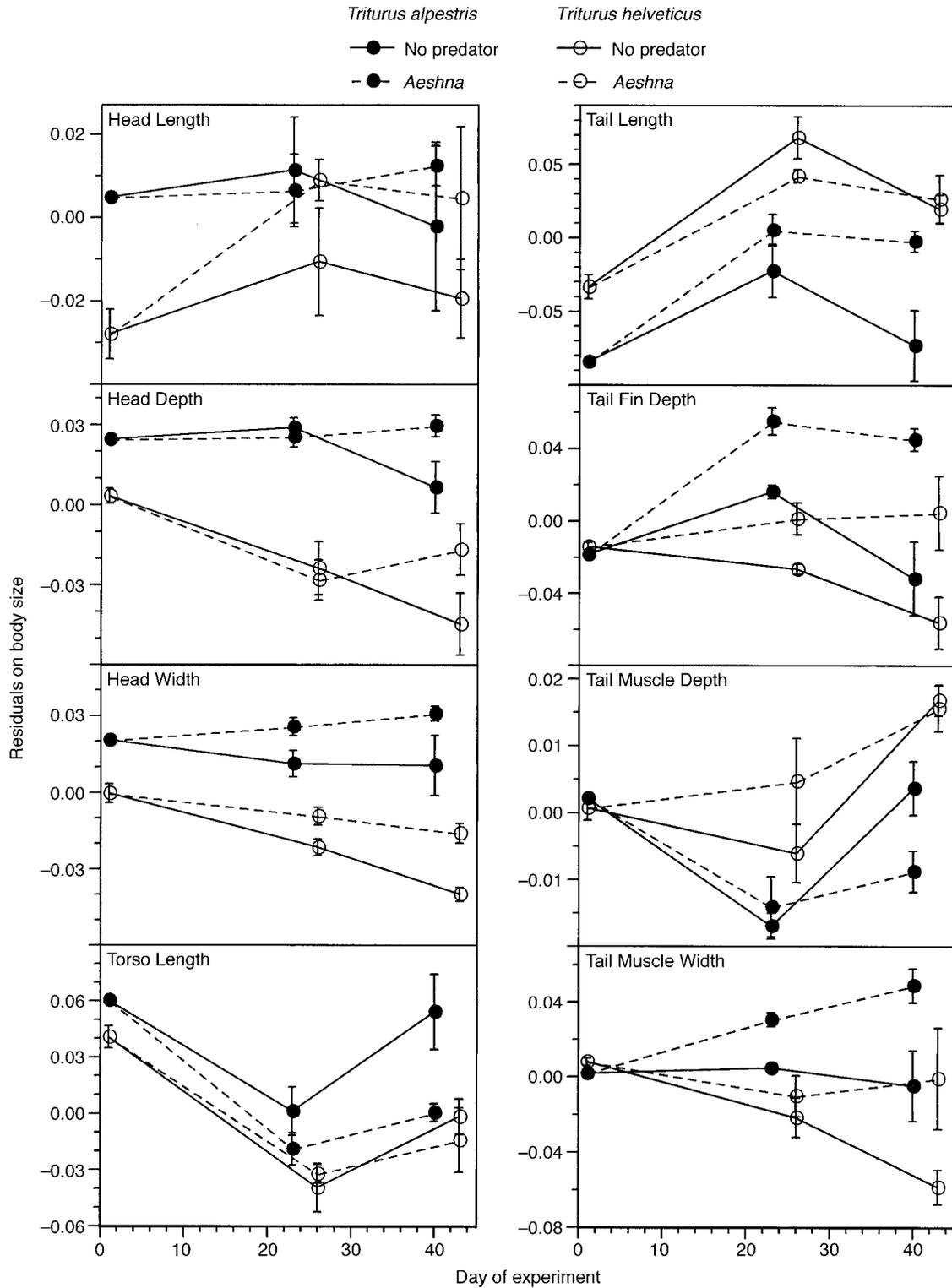
FIG. 5. Developmental changes in size-corrected shape of *Triturus alpestris* and *T. helveticus* larvae in the presence (dashed lines) and absence (solid lines) of caged *Aeshna* dragonfly larvae. Error bars depict ± 1 SE of the mean. When exposed to dragonflies, newt larvae developed larger heads and deeper tail fins. *Triturus alpestris* had a relatively large head and a short tail in comparison with *T. helveticus,* although species differences must be interpreted with caution because the species were reared in separate experiments.

TABLE 4. Multivariate analyses of morphological plasticity of *Triturus alpestris* and *T. helveticus* larvae, measured on days 22–25 and 40–43, in response to environments having either caged *Aeshna* larvae or no predators.

| | | | | Coefficients of the dominant eigenvector | | | | | | | |
Source	df	Wilks' F	P	Head length	Head width	Head depth	Torso length	Tail length	Tail fin depth	Tail muscle width	Tail muscle depth
A) Sample on day 22–25											
Species	8, 5	40.66	0.0004	1.7	34.8	36.5	42.2	24.1	24.7	−7.5	−21.9
Predator environment	8, 5	5.55	0.0376	6.3	23.0	−14.3	−40.9	−28.4	23.4	−1.8	12.1
Species × predator	8, 5	1.80	0.2672	10.4	21.1	40.6	114.9	87.7	5.1	5.9	−18.4
B) Sample on day 40–43											
Species	8, 5	57.20	0.0002	−1.4	42.7	36.2	32.7	4.6	−52.3	37.4	0.7
Predator environment	8, 5	3.33	0.1004	−3.85	−11.1	−29.7	−26.0	−0.5	44.8	−34.5	−28.1
Species × predator	8, 5	5.66	0.0361	7.4	20.1	32.2	34.6	0.1	−48.7	42.3	24.9

Note: The dominant eigenvector represents the linear combination of traits that differed most strongly between predator treatments; traits with positive coefficients were larger in *Triturus alpestris* (species effect) or in the presence of caged-*Aeshna* (predator effect).

sures analyses of the separate traits (Table 2), and by the pattern of shape change shown by these traits during development (Fig. 5). In general, the results of the MANOVA offer the more reliable picture of plasticity because they account for phenotypic correlations among traits.

In principle, the differences between species that we report here may have stemmed from other differences between the 1997 and 1998 experiments, but other evidence suggests that most of these ''species effects'' are real. The faster larval growth rate in *T. alpestris* is
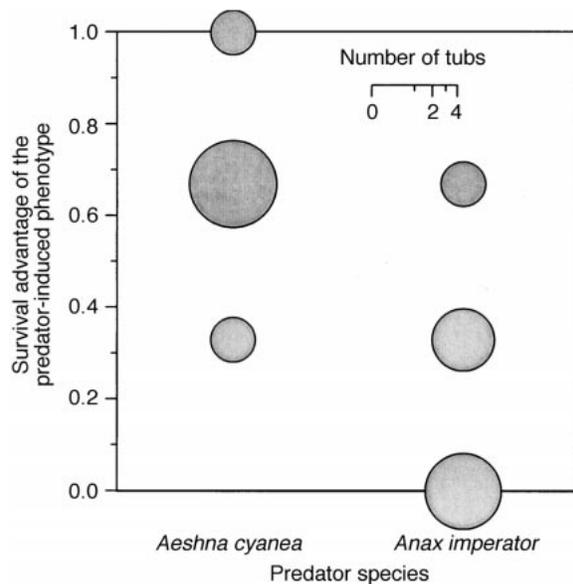

FIG. 6. Survival advantage of the predator-induced phenotype of *Triturus helveticus* larvae when exposed to free predators. The figure depicts results for 12 tubs into which we placed three individuals of each of the two phenotypes. Survival advantage is the difference in survival between the two phenotypes (survival of predator-induced larvae minus survival of no-predator newts). For example, if all three predator-induced larvae survived but none of the no-predator larvae survived, the survival advantage is 1.0.

consistent with its higher activity levels, and occurred even though the *T. alpestris* experiment took place earlier in the spring when growth rate is expected to be slower due to cooler water temperature. Furthermore, the morphological differences are closely similar to patterns observed in the field.

Predation trials: benefits of the phenotypic response to predators

The induced response to dragonflies protected *T. helveticus* larvae from predation. The phenotype induced by previous exposure to *Aeshna* survived the predation trials twice as well as did the no-predator phenotype (Fig. 6, mean survival ± 1 SE: predator-induced larvae, 0.86 ± 0.06; no-predator larvae, 0.42 ± 0.08). Analysis of the difference in survival between the two phenotypes revealed a significant advantage for predator-induced newts, and a difference between the two dragonfly species in the extent to which the predator-induced phenotype survived better ($n = 12$ replicate tubs; intercept term testing whether survival advantage differs from zero: $F = 40.0$, $P = 0.0001$; predator species: $F = 7.4$, $P = 0.0239$). *Anax* killed fewer newts than *Aeshna,* which accounted in part for the smaller survival difference when *Anax* was present (mean ± 1 SD of number killed: *Anax,* 2.0 ± 0.71; *Aeshna,* 2.7 ± 1.21, $P = 0.30$). Alternatively, the pronounced survival advantage of the predator-induced phenotype when exposed to *Aeshna* might have occurred because it was produced by exposure to *Aeshna* rather than *Anax.*

Enhanced survival of predator-induced larvae may have resulted from differences in color, behavior, or morphology. The selection data we present below show that morphological variation affected survival, but we cannot assess additional contributions of behavioral differences because it was impossible to collect individual behavioral observations during the predation trials.
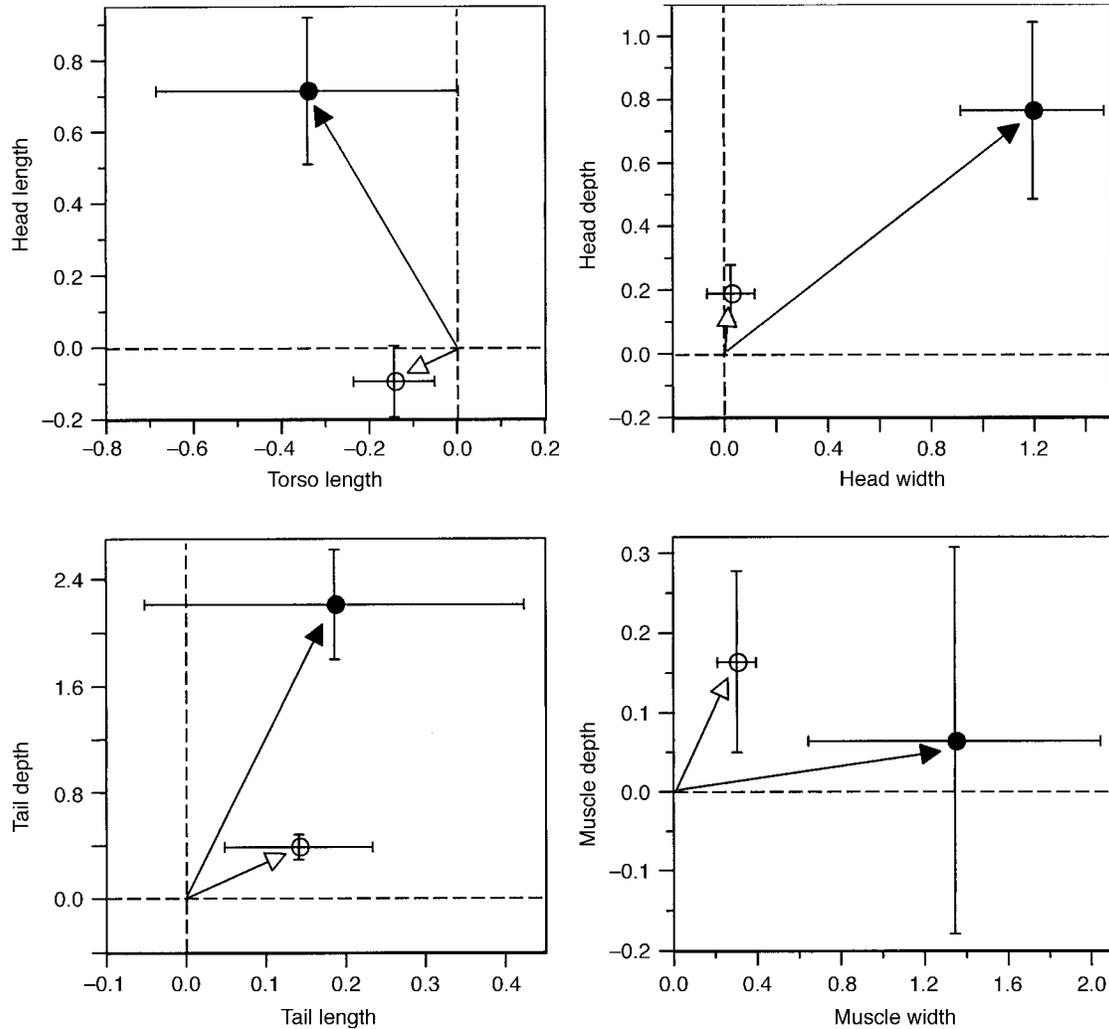
FIG. 7. Comparison between plasticity and selection on size-corrected morphological traits from the head (upper panels) and tail (lower panels) regions of *Triturus helveticus* larvae. Plasticity (solid circle) was measured after 25 days exposure to caged *Aeshna* or no predators in artificial ponds; selection imposed by dragonflies (open circles) was estimated from nonrandom mortality in the predation trial. All coefficients are expressed in terms of standard-deviation units in the no-predator tanks (plasticity coefficients) or prior to selection (selection). The dashed lines represent the case in which the trait is unaffected by selection or plasticity.

Estimates of selection in the presence and absence of predators

Mortality imposed by dragonflies on *T. helveticus* in the predation trials was nonrandom with respect to morphology. To some extent this result was inevitable given the survival advantage of predator-induced newts and the morphological difference between phenotypes. But selection differentials were especially strong for traits in the tail, such as tail depth and muscle width, and rather weak for head/torso traits (Fig. 7). Thus, the pattern of selection imposed by odonates was not identical to the pattern of plastic responses. Multivariate analyses of selection differentials supported this conclusion: the four head/torso measures showed no significant selection, whereas the Intercept term in an anal-

ysis of the four tail measures was nearly significant (Table 5A, B). The Intercept term is the appropriate test for selection in these analyses, because it asks whether the mean selection differential differs from zero. There was no difference between the pattern of selection imposed by *Aeshna* and *Anax* (Table 5).

Two lines of evidence confirmed that tail depth and tail muscle width underwent increasing selection in the presence of dragonflies. First, large positive coefficients for the two traits in the dominant eigenvector from MANOVA on tail shape showed that predation caused a shift toward newt larvae with deeper tails, and wider muscles to a lesser extent (Table 5B). Second, relative tail depth and muscle width were the only two variables to show a significant effect of selection in

TABLE 5. Analyses of selection by dragonflies on *Triturus helveticus* morphology.

A) MANOVA on head shape

				Coefficients of the dominant eigenvector			
Source	df	Wilks' F	P	Head length	Head width	Head depth	Torso length
Selection (intercept)	4, 6	2.21	0.1843	−1.20	1.02	0.94	−0.30
Predator species	4, 6	0.56	0.6987	0.35	1.86	−0.15	1.34

B) MANOVA on tail shape

				Coefficients of the dominant eigenvector			
Source	df	Wilks' F	P	Tail length	Tail fin depth	Tail muscle depth	Tail muscle width
Selection (intercept)	4, 5	4.45	0.0666	0.76	1.62	−0.77	1.05
Predator species	4, 5	1.04	0.4707	0.97	1.68	−1.68	1.10

C) Univariate ANOVA: selection on separate traits

		Response							
Source (df)		Head length	Head depth	Head width	Torso length	Tail length	Tail fin depth	Tail muscle depth	Tail muscle width
Selection (intercept) (1, 9)	F	0.95	4.01	0.05	1.51	1.07	15.23*	1.75	8.71*
	P	0.3545	0.0762	0.8270	0.2510	0.3288	0.0045	0.2182	0.0162
Predator species (1, 9)	F	0.32	1.01	0.11	0.00	0.00	0.18	0.12	1.42
	P	0.5864	0.3422	0.7499	0.9879	0.9967	0.6834	0.7357	0.2635

Notes: Selection differentials were divided by the SD of the trait prior to selection. The dominant eigenvector represents the linear combination of traits most strongly aligned with the source of variation; traits with positive values (for the intercept) underwent increasing selection or (for predator species) showed stronger increasing selection with *Aeshna* than with *Anax*.
  * $P < 0.05$.

univariate tests on the eight separate traits (Table 5C). The result for tail depth is significant after Bonferroni adjustment for eight tests (adjusted $\alpha = 0.0064$).

In the absence of free predators, there was no evidence for selection acting on specific morphological traits (Table 6). The growth cost of responding to predators discussed above demonstrates that selection disfavors individuals possessing the entire suite of predator-induced traits when predators are not actually present, but it does not show that divergent selection on specific plastic traits maintains their flexible response. The regression test for selection within the plasticity

TABLE 6. Multiple regression testing the relationship between morphology and final mass of individual *Triturus helveticus* in the plasticity experiment.

Source	df	Coefficient	F	P
Predator treatment	1	...	9.83	0.0036
Relative head length	1	0.19	0.04	0.8360
Relative head depth	1	1.19	1.66	0.2068
Relative head width	1	0.80	0.34	0.5653
Relative torso length	1	2.18	2.43	0.1287
Relative tail length	1	1.34	2.09	0.1573
Relative tail depth	1	−0.30	0.22	0.6422
Relative muscle depth	1	−0.20	0.02	0.8783
Relative muscle width	1	−0.47	0.59	0.4468
Error	33			

Notes: A positive regression coefficient indicates that relatively high values of the trait were associated with high body mass. This analysis provides no evidence for selection on morphology in the absence of free predators.

experiment confirmed that responding to predators exacted a growth cost (predator treatment in Table 6). However, the nonsignificant relationships between individual morphological traits and growth in this analysis suggest that selection acting on isolated traits was weak or absent.

Predators and morphological variation in nature

We made quantitative samples of newt larvae and their predators within a number of ponds during July 1997 and 1998, because characterizing of the nature of environmental variation is important for understanding the evolutionary maintenance of plasticity. *Triturus helveticus* and *T. vulgaris,* which were not separable from one another in our samples, occurred in 13 and 18 ponds in 1997 and 1998, respectively, and *T. alpestris* occurred in 14 and 25 ponds. Both taxa were found in ponds containing a wide range of densities of predatory insects (Fig. 8). Of the 25 ponds containing *T. alpestris* in 1998, 21 had large aeshnid dragonfly larvae and/or large dytiscid beetles (densities ≤25 individuals/m²), and the remaining four ponds had no predators. Results for *T. helveticus/vulgaris* were similar (Fig. 8). These data show that there is spatial variation in predation regime among newt populations on our study area; such variation may promote the evolution of plasticity (Van Tienderen 1991, Moran 1992).

The abundance of *T. helveticus* was unrelated to that of predators in both years, but *T. alpestris* density was positively related to the density of aeshnid dragonfly
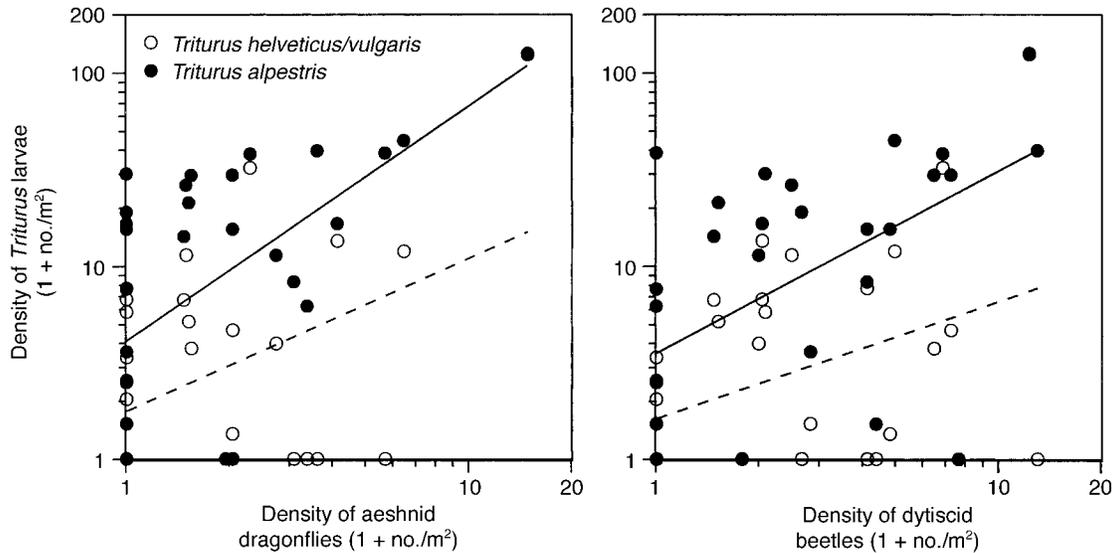
Fig. 8. Distribution of *Triturus* larvae relative to aeshnid dragonflies (*Anax* and *Aeshna* combined) and dytiscid beetles (adults and larvae combined) in 31 ponds near Zürich, Switzerland, during July 1998. Each point depicts the density of newts and predators in a single pond on logarithmic scales. Density estimates were based on ≥20 pipe samples in each pond and include only predators ≥15 mm in body length. Newts were exposed to considerable natural variation in predator densities.

larvae and dytiscid beetles in 1998 (Fig. 8, $r_s = 0.631$, $P = 0.0001$). Newts were found in several ponds in which we captured no predators, but there was no suggestion that they avoided predators. Densities of the two species of *Triturus* were positively correlated ($P = 0.0002$ in both years).

Larval newts of both species exhibited significant variation in head and tail shape across a gradient of predator abundance. We characterized the density of predators in each pond as the sum of the densities of all dytiscids (adults and larvae) and aeshnids, including only individuals ≥15 mm body length. These two groups of predators were the most widespread and abundant within our sample (with the exception of small libellulid dragonflies), and they probably represent the most important mortality risk to amphibian larvae (e.g., Smith 1983). We obtained results similar to those reported here when we performed analyses based on a larger set of predator taxa, including hydrophylid beetle larvae, libellulids, and adult newts, in addition to dytiscids and aeshnids.

Triturus alpestris larvae in the field sample had larger heads than *T. helveticus/vulgaris,* with shorter tails with wider muscles and deeper tail fins (Figs. 9 and 10, Table 7); these differences mirrored those found in the plasticity experiment. Morphological differences between years resulted in part from different methods of preservation: formalin-preserved *T. helveticus/vulgaris* in 1998, and *T. alpestris* in both years, had noticeably swollen heads in comparison with the live-photographed *T. helveticus/vulgaris* in 1998 (Fig. 9). This does not affect the relationship between morphology and predators, which was assessed within

years using newts that were all sampled in the same way. The pattern of variation in head and torso shape among ponds with different predator composition was congruent with the results of the plasticity experiment, with newts in predator-rich habitats having significantly larger heads (Fig. 9, Table 7). The contribution of tail shape to the multivariate response to predator density was different in the two years. Relative tail fin depth and muscle width were larger in predator-rich ponds in 1998, but either did not change or became smaller with increasing numbers of predators in 1997 (Fig. 10). The 1998 results for both tail and head shape may therefore be explained by a combination of plastic responses to predators and selection imposed by predators, as we found in the experiments, but the 1997 results for tail shape are not as predicted by the experiments. In general, though, there is extensive variation in morphology among populations of both species, and much of this variation can be interpreted as plasticity or selection caused by predators.

DISCUSSION

We have shown that *Triturus* newt larvae exhibit predator-induced plasticity in behavior, tail color, and morphology similar to that found in anuran larvae, that the induced response protects newts from hunting dragonflies, and that morphological variation in nature is largely congruent with the experimental results. These findings have two main implications. On the one hand, they extend the taxonomic occurrence of predator-induced plasticity and broaden the scope of plasticity known from salamander larvae. Beyond this, the results illustrate mechanisms underlying the evolutionary
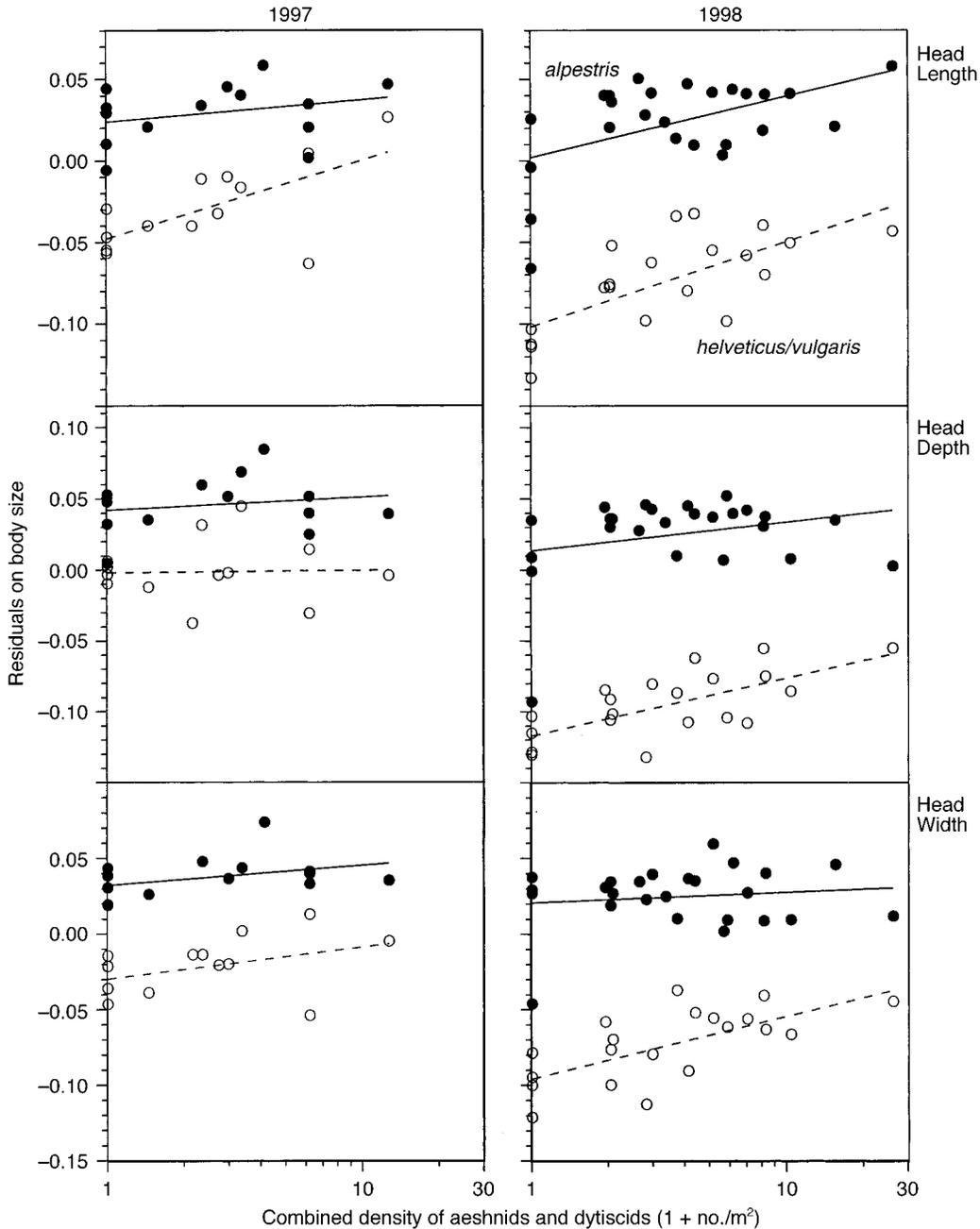
FIG. 9.   Relationships between three of the head shape measurements of *Triturus* larvae and the density of predators in ponds near Zürich, Switzerland, during July 1997 and 1998. Each point shows the mean size-corrected phenotypic value for all newts in one pond, and the density of aeshnid dragonfly larvae plus dytiscid beetles (adults and larvae), including only predators ≥15 mm. Predator density is presented on a logarithmic scale, and results are shown for both *T. helveticus/vulgaris* (open circles) and *T. alpestris* (solid circles).

maintenance of plasticity, and we argue that this evolutionary perspective may be helpful for predicting the occurrence of trait-mediated modification of species interactions arising from phenotypic plasticity.

Phenotypic plasticity in salamander larvae

Triturus newts alter their behavior, tail color, morphology, and life history when dragonflies are present,

and similar predator-induced shifts are widespread in many other amphibians and freshwater invertebrates. The signals that activate phenotypic shifts in newt larvae probably involve water-borne chemicals, as is known for other aquatic organisms (Petranka et al. 1987, Weldon 1990, Dodson et al. 1994, Stabell and Lwin 1997). Physical encounters between newt larvae
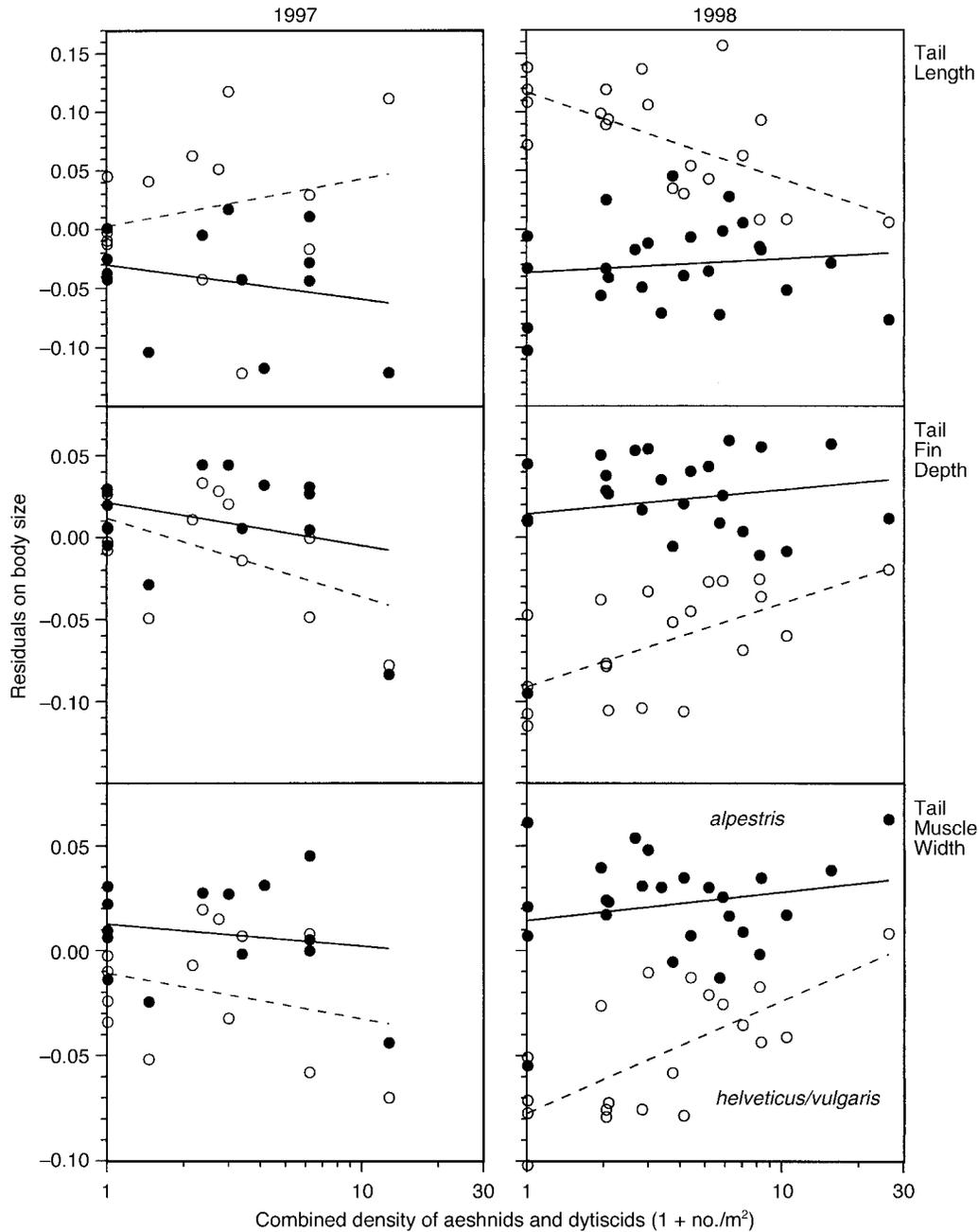
FIG. 10. Relationships between three of the tail shape measurements of *Triturus* larvae and the density of predators in ponds near Zürich, Switzerland, during July 1997 and 1998. Details are explained in the legend of Fig. 9.

and dragonflies were impossible within our experimental ponds, and visual stimuli reaching newts through the cages seem unlikely. Also, Stauffer and Semlitsch's (1993) laboratory experiment with anuran larvae reported that visual and tactile cues signalling the proximity of a predator were less effective than chemical cues.

Nearly all amphibian larvae that have been studied decrease their activity or increase refuge use, and de-

velop relatively deep tail fins and large tail muscles, when they detect insect predators (Sih et al. 1988, Lawler 1989, Van Buskirk 2000). The darkened tail we observed in newts exposed to predators agrees with data from several anurans in the family Hylidae, which develop black or brightly-colored tails in ponds with predators (Caldwell 1982, McCollum and Van Buskirk 1996, Van Buskirk and McCollum 1999).

Plasticity in feeding structures is also well known in

Table 7. Analyses of the relationship between newt morphology and predator density (aeshnids and dytiscids combined) in ponds near Zürich, Switzerland, during 1997 and 1998.

A) MANOVA

				Coefficients of the dominant eigenvector							
Source	df	Wilks' F	P	Head length	Head depth	Head width	Torso length	Tail length	Tail fin depth	Tail muscle depth	Tail muscle width
Year	8, 55	5.82	0.0001	−0.90	4.08	−0.38	−1.22	−1.14	0.55	5.05	−2.27
Species	8, 55	19.81	0.0001	1.19	−0.62	7.04	0.21	−0.19	−2.73	−3.17	1.66
Predator density	8, 55	5.55	0.0001	5.10							

B) Univariate ANOVAs

	Response							
Source (df)	Head length	Head depth	Head width	Torso length	Tail length	Tail fin depth	Tail muscle depth	Tail muscle width
Year (1, 62)	16.59* (0.0001)	37.86* (0.0001)	21.36* (0.0001)	1.86 (0.1771)	7.49* (0.0080)	14.82* (0.0003)	18.89* (0.0001)	8.37* (0.0052)
Species (1, 62)	86.46* (0.0001)	57.58* (0.0001)	117.98* (0.0001)	6.45* (0.0135)	27.96* (0.0001)	17.76* (0.0001)	0.00 (0.9803)	29.50* (0.0001)
Predator density (1, 62)	21.34* (0.0001)	3.07 (0.0855)	8.24* (0.0055)	0.00 (0.9916)	0.73 (0.3973)	0.04 (0.8447)	4.50* (0.0377)	0.88 (0.3506)
Species × predator (1, 62)	0.52 (0.4720)	0.21 (0.6519)	1.10 (0.2990)	0.24 (0.6282)	0.34 (0.5604)	0.01 (0.9209)	0.31 (0.5773)	0.33 (0.5685)
Year × predator (1, 62)	1.13 (0.2921)	1.91 (0.1711)	0.31 (0.5806)	0.38 (0.5390)	1.00 (0.3204)	8.77* (0.0043)	4.38* (0.0403)	7.09* (0.0097)

Notes: The dominant eigenvector represents the linear combination of traits most strongly aligned with the source of variation; traits with positive values (for year) were larger in 1998, (for species) were relatively large in *T. alpestris,* or (for predator density) were larger in ponds with many predators. In (B), the table presents F values, with P values in parentheses.
* $P < 0.05$.

salamander larvae. Changes in head shape can be induced by diet or density (Walls et al. 1993, Nishihara 1996), and may be related to onset of cannibalistic behavior (Collins and Cheek 1983, Maret and Collins 1997). Our results for external morphology, in combination with the earlier studies of plasticity in trophic morphology, behavior, and life history, suggest that many aspects of salamander phenotypes are potentially flexible. The adaptive basis of these phenotypic shifts is not always clear, and cannot be assumed simply because plasticity seems to be beneficial. Before concluding that a trait is adaptive, one must test whether it is beneficial for individuals that express it and whether it is currently maintained by selection (Williams 1992, Brandon and Rausher 1996).

Adaptive plasticity: environmental heterogeneity and individual performance

Two features common to most models for the evolution and maintenance of plasticity are environmental variation that enforces a fitness trade-off and the availability of a cue reflecting the condition of the environment (Levins 1968, Via and Lande 1985, Van Tienderen 1991). Both are fulfilled for *Triturus* newts on our study area. The field results document the extent of spatial variation in predator abundance across 25–30 ponds during 1997 and 1998: newt larvae occur in ponds with predator densities ranging from 0 to >20 predators/m² (Figs. 8, 9, and 10). Further sampling will be required to quantify the magnitude of temporal variation, which

is especially effective at maintaining plasticity (Moran 1992), but data from other freshwater systems indicate that predators are often heterogeneous in time (Jefferies 1994, Schneider 1997). The field data also suggest that newt larvae naturally exhibit different phenotypes in response to variation in predation regime, and this was especially true for head shape.

Our results indicate that variation in predator abundance could establish a fitness trade-off, with each phenotype performing better under the predation regime that induced it than do other phenotypes. The evidence for a performance difference between phenotypes is stronger for the environment containing dragonflies than for the environment without predators: the predator-induced phenotype survived about twice as well as the no-predator phenotype in predation trails with free dragonfly larvae.

It could be argued that the benefits of possessing the predator-induced phenotype are less dramatic in nature than our results suggest, for at least two reasons. First, encounter rates between newt larvae and their predators may be higher in experimental tubs than in natural ponds. This is unlikely to be true if encounter rates are a function of densities, because many ponds on our study area have predator and newt densities far higher than we used in the predation trial (Fig. 8). Second, larvae that survive predation in natural ponds may experience release from competition and therefore grow and develop more rapidly (Slobodkin 1962, Wilbur 1988). This possibility also seems unlikely since the

benefits from thinning will rarely compensate for the decreased probability of survival (Van Buskirk and Yurewicz 1998). We conclude that the predator-induced phenotype performs better than the no-predator phenotype in the presence of dragonflies, and that this difference would probably be enforced under natural conditions as well.

In the absence of predators the two phenotypes survived equally well, and evidence for a growth or developmental cost of responding to predators was mixed. *Triturus helveticus* grew especially slowly in the presence of odonates, when sampled just before the onset of metamorphosis. Slow larval growth has been associated with decreased adult fecundity in other salamanders (Semlitsch et al. 1988, Scott 1994), but even if decreased growth is not directly tied to adult performance it may be risky to remain small for an extended period in ponds with predators (Wilbur 1988, 1997). Thus, in *T. helveticus* the phenotype that performed best in the predator-free environment was the one that was induced by that environment.

The relative performances of the two phenotypes in the absence of predators was less clear for *T. alpestris,* which responded to caged predators with a combination of delayed metamorphosis, slightly reduced growth and development rates, and emergence at larger body size. The net effect of these changes is uncertain without information on the sensitivity of fitness to simultaneous variation in size and timing of emergence (e.g., Smith 1987); we are therefore uncertain whether the predator-induced phenotype is costly in *T. alpestris.* However, if the benefits of larger size at metamorphosis are outweighed by costs of delayed development, then predator-induced *T. alpestris* would experience reduced fitness in predator-free environments, and evidence would support the maintenance of plasticity by a fitness trade-off across the predation gradient. In this case, newt larvae displaying plastic responses to predators would have higher fitness than would individuals that do not exhibit plasticity. This interpretation seems plausible in light of the widespread costs of predator-induced phenotypes in larval anurans (Van Buskirk 2000).

Similar arguments apply to the issue of whether selection maintains plasticity in specific morphological traits in *Triturus* larvae. We found that aeshnids imposed strong selection on tail shape traits, and this makes good sense from a functional standpoint. Kinematic analyses of fast starts by larval salamanders and small fishes show that the entire sequence of predator escape consists of two sudden swings of the tail, first one way and then the other (the ''C-start;'' Blight 1977, Webb 1984, Hale 1996, Dommenici and Blake 1997). We measured a >13% increase in tail depth in the presence of predators for both newt species; the additional surface area afforded by increased tail depth may provide a significant improvement in propulsion. In anuran tadpoles, tail morphology is correlated with

swimming stamina and acceleration (McCollum and Leimberger 1997). Thus, the directional selection gradient in ponds with predators is consistent with the interpretation that natural selection maintains plasticity in *Triturus* tail fin and muscle.

If plasticity in tail shape is currently maintained by selection then we expect to find selection acting against predator-induced tail morphology when predators are absent; we instead found no evidence for selection on tail morphology in cattle tanks without free predators. Similar results come from studies of other taxa, suggesting that weak selection in predator-free habitats or weak costs of responses to natural enemies are widespread (Brown 1988, Spitze 1992, Karban 1993, Van Buskirk and Relyea 1998). In fact, many circumstances could account for weak selection on tail morphology in predator-free ponds without disqualifying an adaptive interpretation of plasticity (Van Buskirk and Relyea 1998). Theoretically, induced defenses might be maintained by weak or sporadic divergent selection across predator environments if there are only limited fitness costs of plasticity itself (Van Tienderen 1991). There is a clear need for theoretical and empirical work on the costs of plasticity and the issue of how strong or how often selection must be in place to maintain plasticity (Via et al. 1995).

The question of whether or how selection promotes plasticity in head shape remains unanswered. The size of the head is probably related to prey capture in salamanders (Zaret 1980), and polymorphisms in many other species have a relatively straightforward adaptive interpretation because plasticity produces a close association between trophic morphology and a locally available resource (Collins and Cheek 1983, Walls et al. 1993, Loeb et al. 1994, Nishihara 1996). We propose that predator-induced variation in *Triturus* head shape may also be adaptive because it improves feeding efficiency in both environments. Our hypothesis is based on the observation that *Triturus* occupy different microhabitats in the presence and absence of predators (Fig. 3): newts in predator-free ponds often feed on small zooplankton in the water column, while those in the presence of predators spend a disproportionate amount of time in the benthos where larger prey predominate (e.g., chironomids and snails). Selection may favor newts that develop wide heads when predators are present because they can more effectively capture the larger prey taxa they encounter in refuge habitats. Our hypothesis suggests that plasticity is maintained by selection related to feeding, but the cue that elicits the response (predation) is not directly related to the agent of selection (size of prey). The fitness components affected by selection for improved feeding rates would include growth and development, rather than survival, which explains why we did not observe selection on head shape during the short time frame of the predation experiment.

Whatever its adaptive basis, plasticity in head shape

of larval newts is a remarkably indirect response to predators. Predator-induced phenotypes nearly always reduce mortality during an attack by a predator, or at least their design is consistent with a defensive interpretation (Harvell 1990, Tollrian and Harvell 1999). Induced variation in *Triturus* head shape is different because predators do not impose selection on head shape and it has no plausible direct defensive function: once a newt is detected and attacked by a predator the larger head is of no advantage. This sort of indirect adaptive plasticity is uncommon or unknown, so far as we are aware, and would be well worth testing.

Plasticity and species interactions

Data on the adaptive basis of plasticity may help predict conditions under which community theory should incorporate shifting interaction strengths resulting from plasticity in species' traits. Several examples illustrate that interaction strengths are modified by changes in traits of the species that are involved (Wissinger and McGrady 1993, Wootton 1993, Peacor and Werner 1997, 2000). In amphibians, behavioral and morphological responses to predators can increase resistance to predators (Van Buskirk and McCollum 1999), increase an individual's competitive impact on other species (Werner and Anholt 1996), and change population size structure, which can in turn influence species interactions (Polis 1991, Werner 1994). Induced phenotypic changes seem most likely to alter species interactions when they involve traits which simultaneously influence vulnerability to predators and resource use, and for this reason feeding activity has been a particular focus of interest (Wissinger and McGrady 1993, Werner and Anholt 1996, Abramsky et al. 1998). While the empirical results demonstrate the potential quantitative importance of phenotypic shifts, theoretical studies show that these effects can qualitatively alter community structure and dynamics (Abrams 1995, Matsuda et al. 1995).

These observations raise two separate questions: (1) When do organisms exhibit plasticity in traits that are involved in species interactions?; and (2) How often does plasticity alter the strengths of species interactions? The second question is not directly addressed by studies such as ours, but an evolutionary perspective can help answer the first question by identifying the conditions under which plasticity evolves and is maintained by selection. Evolutionary studies suggest that species interactions occurring with highly variable intensity will promote or maintain plasticity, especially within habitats that can transmit a reliable cue to betray the presence of natural enemies or competitors (Harvell 1990, Karban and Baldwin 1997). These conditions are often met in freshwater aquatic habitats, and in fact nearly every group of freshwater metazoan that has been studied shows predator-induced morphological plasticity (Tollrian and Harvell 1999). Further, a sizeable fraction of all known cases of trait-mediated indirect effects comes from freshwater systems (Huang and Sih 1990, Turner and Mittelbach 1990, Wissinger and McGrady 1993, Werner and Anholt 1996, Peacor and Werner 1997). Although there may be a bias toward studying induced defenses in aquatic communities, these results broadly concur with predictions stemming from evolutionary studies of plasticity.

Our approach helps connect ecological perspectives on species interactions with evolutionary perspectives on phenotypic design. The ecological context of adaptation has been appreciated by evolutionists since the time of Darwin, but insights from evolutionary biology have been employed less widely within community ecology. We hope that our results can be combined with studies of other freshwater organisms to demonstrate the general occurrence of predator-mediated plasticity in these habitats, the mechanisms that help maintain plasticity, and the role of plasticity in modifying species interactions within aquatic foodwebs.

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APPENDIX

A complete map of the morphometric landmarks for *Trituris alpestris* and *T. helveticus* is available in digital form in ESA's Electronic Archive: *Ecological Archives* E081-025.