

Feeding Performance in Heterochronic Alpine Newts is Consistent with Trophic Niche and Maintenance of Polymorphism

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Abstract

The feeding performances of two heterochronic morphs of the Alpine newt *Triturus alpestris* were investigated in laboratory experiments. Although both morphs are able to feed in the aquatic habitat, the hydrodynamics of prey capture differ between morphs. In paedomorphs water sucked with prey is expelled behind the mouth through gill bars. In metamorphs, water is expelled by the mouth as gill slits are closed. Feeding performance was better in paedomorphs than in metamorphs when foraging on aquatic crustaceans, but paedomorphs were less successful when foraging on terrestrial invertebrates caught at the water surface. These differences in prey capture success related to prey type allow the two morphs to use specific resources in their aquatic habitat. These results are consistent with previous studies that showed diet differentiation between morphs in natural populations. Such resource partitioning is a factor favouring the maintenance of facultative paedomorphosis in natural populations.

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Introduction

Trophic polymorphisms are characterized by discrete morphs showing differential resource use (Skulason & Smith 1995). They have been observed principally in fishes (Hindar & Jonsson 1982; Meyer 1990; Malmquist et al. 1992; Robinson 2000), but also in amphibians (Collins & Holomuzki 1984; Denoël & Joly 2001) and birds (Smith 1990). In fishes, variation in diet between alternative morphs was shown to be related to the variation of the performance of their trophic apparatus (Liem & Kaufman 1984; Lavin & McPhail 1986; Meyer 1989; Malmquist 1992), but the situation remains unclear in amphibians.

In newts and salamanders, facultative paedomorphosis is a suitable process to explore the evolutionary ecology of trophic polymorphisms because it results in the coexistence of morphs that differ in several traits such as the physical mechanisms of prey ingestion. These differences in feeding mechanisms begin at metamorphosis. Accordingly, the aquatic feeding mechanism shifts from a unidirectional to a bi-directional hydrodynamic system. In the larvae, the water taken with the prey is expelled through the gill bars at the posterior part of the mouth cavity in a unidirectional flow. After the gill slits become closed at metamorphosis, the water taken with a prey is expelled through the mouth

while the prey is kept within the oral cavity by the tongue, the eyes and the teeth (Joly 1981; Lauder & Shaffer 1993). Paedomorphosis results in a delay of metamorphosis and retention of the unidirectional feeding mechanism in adults (Semlitsch & Wilbur 1989; Whiteman 1994). The overall performance of the feeding apparatus differs according to morphology, with the larval structure of the trophic apparatus being more efficient (Whiteman et al. 1996). The closing of the gill slits and the reduction of muscle mass at metamorphosis alter the efficiency of prey snapping under water (Lauder & Reilly 1988; Lauder & Reilly 1990). However, no studies directly compared the diet and success rate of prey capture in syntopic alternative morphs of newts and salamanders from the same population.

In the Alpine newt, sexual performance and courtship patterns are similar in the two morphs (Denoël et al. 2001b; Denoël 2002), but paedomorphs may take advantage of their ontogenetic status in reaching maturity at a younger age than metamorphs (Denoël & Joly 2000) and in obtaining high-energy intake from their food and life habits (Denoël et al. 2002). In a French Alpine lake, Denoël & Joly (2001) found that metamorphic Alpine newts inhabit only the shoreline and shallow areas, while paedomorphs use all micro-habitats including the entire water column and deep benthic areas. Diets reflected this difference in habitat use as paedo-

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morphs mainly foraged on planktonic prey such as water fleas and fairy shrimps whereas metamorphs mainly foraged on terrestrial insects that had fallen on the water surface (Denoël & Joly 2001).

My aim was to compare the snapping behaviour performance of paedomorphic and metamorphic Alpine newts with regard to different prey types. These prey types were selected with respect to diet variations that were observed in a natural population in which feeding habits have been previously determined (Denoël & Joly 2001). Given the natural diet of the alternative morphs in their lake, I expected the paedomorphs to be more efficient than the metamorphs when foraging on aquatic prey (such as planktonic crustaceans like water fleas and fairy shrimps, and potentially aquatic insects) but to be less efficient than the aquatic metamorphs when foraging on large insects (such as flies) that had fallen on the water surface.

Methods

Study Organisms

I caught 20 paedomorphic Alpine newts *Triturus alpestris* (Laurenti, 1768) (10 males and 10 females) in La Cabane Lake in Oct. 1999 (Southern French Alps; 47°24'N/6°24'E Greenwich; altitude of 1950 m a.s.l.) where the two morphs coexist (Denoël et al. 2001a). In this population, the two morphs differed neither by age nor by size (Denoël & Joly 2000). Adulthood was determined on the basis of a developed cloaca, and sex on the presence of secondary sexual characters (e.g. dorsal crest, colour, and shape of the cloaca; Denoël et al. 2001b). I kept the newts in refrigerated boxes (5–10°C; 30 × 20 cm and 12 cm high) to transport them to the laboratory.

Experimental Procedure

The principle of the experimental design was to compare the feeding behaviour of paedomorphic newts with the feeding behaviour they exhibited after they had completed metamorphosis, i.e. when they became metamorphs. Both paedomorphs and metamorphs are mature individuals (Denoël et al. 2001b).

Newts were kept in two aquaria (250 × 30 cm and 35 cm high; 10 individuals in each) for 3 mo. Temperature was 14°C and photoperiod was LD 14/8 h. Individual identification was ensured by toe-clipping (Twitty 1966). Because of the low number of newts, only one toe was clipped. Toe-clipping has been shown not to affect survival and body condition of *Triturus* (Arntzen et al. 1999).

The trials started 1 wk after the arrival of the newts in the laboratory. The trials consisted of three different phases. The first was a 3-d habituation period where the newts were fed with the prey type used in the subsequent test. The second was a 2-d starvation period where no food was provided. The third was the test period where the performance of the newts was measured. In this test, an individual newt was put in an aquarium (50 × 25 cm and 30 cm high) in which the bottom was covered with gravel. Temperature was 14°C and illumination was 5000 lux on the bottom of the aquarium. Five minutes after the introduction of a newt, a fixed quantity of prey items was introduced into the aquarium (see next paragraph), which means that each individual received the same amount of food all at once (one kind of prey per trial). The behaviour of the newt was then recorded during 20 min by encoding data on a computer. I took three behavioural variables

into account: capture attempts, successful and failed captures. A capture attempt corresponds to suction and/or snapping behaviour towards a prey. A capture was considered to be successful if the newt managed to catch and swallow the prey. After each trial, prey items were removed and the water was replaced. A new trial was then started with another newt. Each trial involving a male was followed by a trial using a female to avoid any time effect on the outcome of the experiment (a time effect might have been produced if trials with males occurred at a different time of day than trials with females). Newts were taken randomly from the maintenance aquaria.

The above procedures were repeated four times using different prey types in the following order: water fleas (0.4 g of *Daphnia magna*), fairy shrimps (0.4 g of *Artemia salina*), insect larvae (0.4 g of *Chironomus plumosus*) and flies (0.2 g of *Lucilia* sp.). Prey were weighed rather than counted to avoid wounds during manipulation. Prey quantities were around 500 for *Daphnia*, 40 for *Artemia*, 110 for *Chironomus*, and 10 for *Lucilia*. Prey item sizes (length and width) were around 2 × 1 mm for *Daphnia*, 8 × 2 mm for *Artemia*, 9 × 1 mm for *Chironomus* and 8 × 3.5 mm for *Lucilia*. Newts are natural predators of these four kinds of prey in their lake and consequently were already experienced in capturing them before the experiment (Denoël & Joly 2001). Gape size was measured for each individual at the start of the trial and after metamorphosis. It corresponds to the maximal distance between the left and right sides of the mouth opening.

After completion of the 80 trials, paedomorphic newts were kept in the two maintenance aquaria, but without water to induce metamorphosis. The substratum of the aquaria consisted of wet gravel. All paedomorphs had metamorphosed after 40 d. One week after the last newt had metamorphosed, I repeated the trials with these metamorphic newts.

All newts were released in their native lake after completing the experiment.

Statistical Analysis

I used a General Linear Model (multi-way within-subject manova) to test for an effect of morph, sex, prey and their interactions on the success rate of capture (i.e. the ratio between the number of capture attempts and that of ingested prey), the number of capture attempts and the number of ingested prey. Because I induced metamorphosis of paedomorphs and because the four kinds of prey were given to the same 20 individuals, the data were not independent. I thus took into account two levels of repeated measurements in the model (within-morph for the four kinds of prey and between morphs for the observations before and after metamorphosis). I used square-root (+0.5) transformation of the count data to meet the assumption of anova (Sokal & Rohlf 1995). Because some cells are missing for the capture rates (individuals that did not try to catch prey), presented degrees of freedom are lower than those for a full table. Planned pair-wise comparisons between morphs for each kind of prey were computed with a protected LSD-test (Day & Quinn 1989). The comparisons are planned because of field observations suggesting differences between morphs (Denoël & Joly 2001). All tests were made with Statistica and used $\alpha = 0.05$ (Statsoft-France 2000).

Results

Morph and prey have a significant effect on the three analysed variables: success rate of capture,

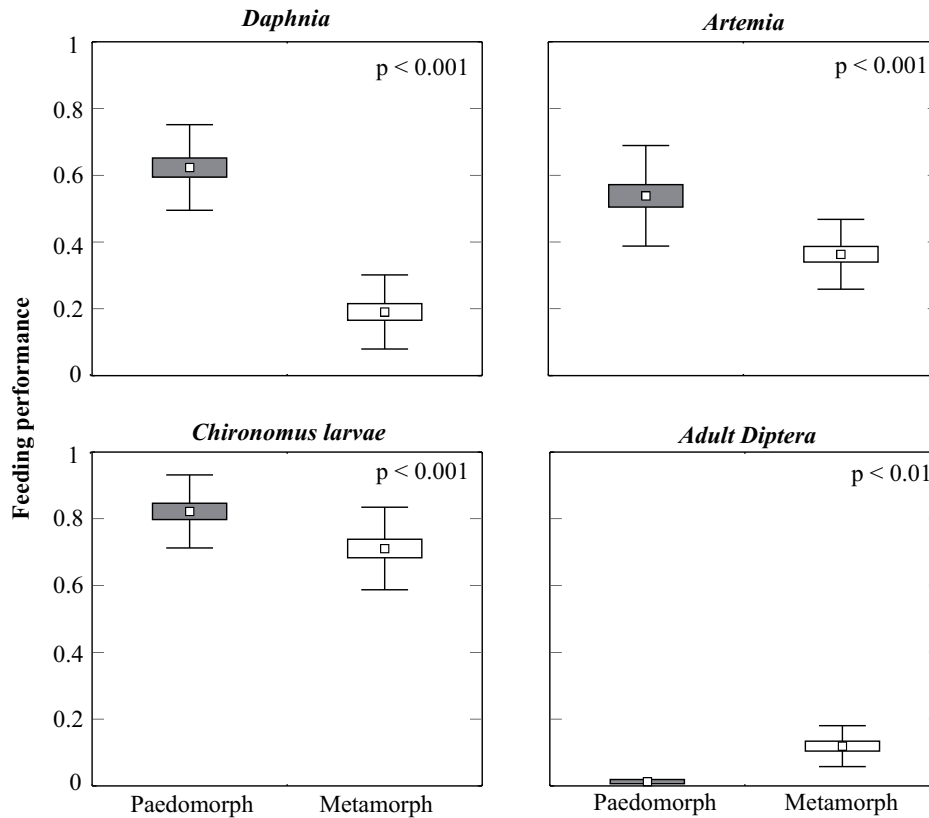


Figure 1: Feeding performances (rate of successful captures) of newts in 20-min trials. P, paedomorphs (shaded boxes); M, metamorphs (white boxes). Dots, mean; boxes, SE; whiskers, SD. The statistical comparisons were performed by a protected LSD test after anova (see Table 1). $n = 20$ in each group

number of capture attempts and number of ingested prey (manova: Wilk's $\lambda = 0.023$, $F_{3,8} = 112.737$, $p < 0.001$ and $\lambda = 0.001$, $F_{9,2} = 179.952$, $p < 0.01$ respectively), but sex has not ($\lambda = 0.798$, $F_{3,8} = 0.676$, $p = 0.59$). Interactions between morph and prey are significant ($\lambda = 0.007$, $F_{9,2} = 31.359$, $p < 0.05$), but the three others interactions are not (morph \times sex: $\lambda = 0.825$, $F_{3,8} = 0.567$, $p = 0.65$; prey \times sex: $\lambda = 0.080$, $F_{9,2} = 2.526$, $p = 0.312$; morph \times prey \times sex: $\lambda = 0.094$, $F_{9,2} = 2.137$, $p = 0.36$).

Morph, prey and the interaction between these two variables have a significant effect on the success rate of prey capture (anova, $p < 0.001$, Table 1). Paedomorphs and metamorphs significantly differed in the success rate of prey capture for the four kinds of prey (anova: protected LSD test): *Daphnia* ($p < 0.001$; Fig. 1), *Artemia* ($p < 0.001$; Fig. 1), *Chironomus* larvae ($p < 0.001$; Fig. 1), and adult Diptera ($p < 0.01$; Fig. 1). The success of paedomorphs was higher for all prey except adult flies.

All four prey types were preyed by the different categories of newts: paedomorphic and metamorphic, males and females. All individuals exhibited catching behaviour on *Daphnia*, *Chironomus* larvae and *Artemia*. Only 12 paedomorphs of 20 and 18 metamorphs of 20 foraged on adult Diptera. The three former prey types were caught on the bottom of the aquarium (by suction), while the flies were snapped at the water surface. The newts that did not forage remained on the floor of the aquarium. Morph (anova, $p < 0.05$, Table 1), prey ($p < 0.001$) and the interaction between these two variables ($p < 0.01$) have a significant effect on the number of capture attempts. Metamorphs tried to catch more *Artemia* than paedomorphs during the 20-min trials (mean \pm SE = 37.3 ± 3.3 and 19.2 ± 2.4 , respectively; anova: LSD test, $p < 0.001$), but no significant difference was observed between morphs for the three other kinds of prey (*Daphnia*, *Artemia* larvae and adult Diptera).

Morph (anova, $p < 0.01$, Table 1), prey ($p < 0.001$) and the interaction between these two variables ($p < 0.001$) have a significant effect on the number of ingested prey. The two morphs differed significantly in this respect for the four types of prey (anova: protected LSD test). During the 20-min trials, scores were higher in paedomorphs than in metamorphs for the ingestion of *Daphnia* (mean \pm SE = 23.5 ± 2.3 and 9.0 ± 1.3 , respectively; anova: protected LSD test, $p < 0.001$) and *Chironomus* larvae (mean \pm SE = 36.5 ± 2.2 and 27.4 ± 1.9 , respectively; anova: protected LSD test, $p < 0.001$), but lower for *Artemia* (mean \pm SE = 10.3 ± 1.4 and 13.0 ± 1.0 , respectively; anova: protected LSD test, $p < 0.05$) and adult Diptera (mean \pm SE = 0.2 ± 0.1 and 1.3 ± 0.2 , respectively; anova: protected LSD test, $p < 0.001$).

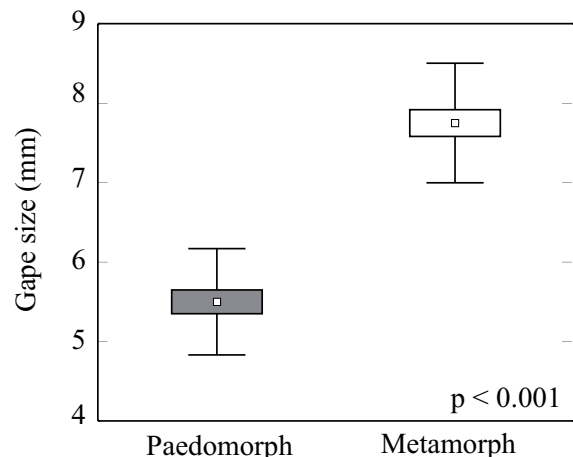


Figure 2: Gape size of newts before and after metamorphosis. P, paedomorphs (shaded boxes); M, metamorphs (white boxes). Dots, mean; boxes, SE; whiskers, SD. The statistical comparison was performed by anova with repeated measurement procedure in the General Linear Model. $n = 20$ in each group

Table 1: Analysis of variance for morph and prey effects on success rate of prey capture, number of capture attempts, and number of successful captures per trial. Factors have been analysed with a repeated measurement procedure in the General Linear Model

Trait	Source	df	F	p
Success rate	Morph	1,11	50.590	<0.001
	Prey	3,33	271.301	<0.001
	Morph × prey	3,33	32.099	<0.001
Capture attempts	Morph	1,19	6.479	<0.05
	Prey	3,57	49.080	<0.001
	Morph × prey	3,57	5.739	<0.01
Successful captures	Morph	1,19	15.100	<0.001
	Prey	3,57	238.385	<0.001
	Morph × prey	3,57	12.856	<0.001

There was a significant effect of morph on the width of the mouth opening (anova, $F_{1,18} = 155.769$, $p < 0.001$), but sex and the interaction between morph and sex were not significant (anova, sex: $F_{1,18} = 3.212$, $p = 0.08$; interaction: $F_{1,18} = 0.077$, $p = 0.79$). Metamorphosis resulted in a widening of the mouth opening: from a mean of 5.5 mm (SE = 0.2 mm) in paedomorphs to 7.8 ± 0.2 mm in metamorphs (Fig. 2). This increase in gape size resulted from the regression of the labial folds at the edges of the mouth opening.

Discussion

This study demonstrates that trophic performances differ between heterochronic morphs in Alpine newts and are directly related to the pattern, which was observed in the field in another study (Denoël & Joly 2001). The success rate of Alpine newts preying on aquatic organisms is higher in paedomorphs than in recent metamorphs. A previous study showed that the alternative morphs of another heterochronic species (*Ambystoma tigrinum*) also differed in feeding efficiency, but with only one morph (the paedomorph) at the advantage (Whiteman et al. 1996). In contrast, in this study, the success rate for feeding on terrestrial invertebrates caught at the water surface (adult flies here) was higher in metamorphs.

Differences in capture efficiencies are directly related to the trophic system of the newts. The best performance of metamorphs feeding on large prey, such as Diptera, can be related to their larger mouth opening. At metamorphosis, labial folds regress and allow the newts to ingest large prey items. Paedomorphs are thus constrained to catch small prey. However, the hydrodynamics of paedomorph predation relies on unidirectional water flow: water is drawn into the mouth by suction and then expelled backwards through the gill slits. Experimental obstruction of gill slits has shown that this unidirectional system results in higher prey capture efficiency (Lauder & Reilly 1988). Moreover, the decrease of the muscle mass of the trophic apparatus at metamorphosis lowers the performance of capture (Lauder & Reilly 1990). The larval trophic system is thus more efficient for the capture of aquatic prey than the metamorphosed one (Reilly & Lauder 1988; Whiteman et al. 1996).

Another difference between paedomorphs and metamorphs lies in the presence of gill rakers in paedomorphs. These structures could facilitate prey capture in two different ways. First they could favour the retention of small prey, such as water fleas (Lauder & Reilly 1994). It was shown in polymor-

phic species of fish, that pelagic morphs have longer gill rakers than benthic morphs, which increase their prey capture success when feeding on plankton organisms (Amundsen 1988; Malmquist 1992). In addition to the retention of prey, gill rakers improve the suction mechanism as they prevent the entrance of water through the gill slits (Lauder & Reilly 1994).

Although less efficient than paedomorphs in the capture of crustaceans, metamorphs show a similar interest for water fleas as do paedomorphs and an even higher interest for fairy shrimps. Overall, in the laboratory experiment, paedomorphs ingested a larger number of *Daphnia* and chironomid larvae than metamorphs, but a lower number of *Artemia* and adult Diptera. The interest for large prey items probably relies on the large biomass of these organisms comparing with the very small one of daphnids. However, in natural lakes, small prey organisms are usually the most abundant. The presence of voluminous terrestrial invertebrates, which fall at water surface, constitutes an important nutritional input in mountain lakes. Metamorphic newts are well known for foraging on these prey items (Chacornac & Joly 1985; Joly & Giacoma 1992). Nevertheless, the presence of these exogenous invertebrates is limited in number and time (Denoël & Joly 2001), making small prey the only available resource at some time of the year.

In the present experimental design, the order of prey items was not randomized. It is unlikely that prey capture efficiencies might have been significantly affected. First, the experiment was based on adults, and thus on old individuals (at least 4–5 yr: Denoël & Joly 2000) that have already gained experience in natural conditions with the four kinds of prey of the experiment. Secondly, the low success in catching crustaceans and chironomid larvae in metamorphs shows that individual experience did not increase success.

Resource polymorphisms are suspected to evolve in heterogeneous or unpredictable environments where each morph can specialize on specific resources (Smith & Skulason 1996). Because the two morphs differed by their feeding performances with respect to different prey types, they are expected to segregate in their use of resources. Indeed, there was a substantial resource partitioning between the two morphs with paedomorphs mainly preying on plankton (six times more frequently than metamorphs) and metamorphs mainly preying on terrestrial prey, which had fallen on the water surface (two times more than paedomorphs) (Denoël & Joly 2001). This study constitutes thus the first connection between trophic morphology (open and closed

gill slits), trophic performance (success of prey capture) and diet in natural populations of polymorphic species of newts and salamanders.

Densities of planktonic and terrestrial invertebrates are not homogeneous within aquatic habitats. In some microhabitats, such as the water surface, terrestrial invertebrates are particularly abundant while they are scarce in the deepest part of lakes and in the water column, where planktonic organisms predominate. Similarly, space partitioning between the two morphs was shown in La Cabane Lake, with metamorphs abundant at the water surface and along the shoreline, whereas paedomorphs were present in all microhabitats (Denoël & Joly 2001).

Both food and habitat partitioning suggest that feeding performance and optimality rules of decision may trigger these differences in diet choice between morphs. A detailed study of the energetic balance of foraging on different prey types and of the constraints imposed by each micro-habitat would be needed to understand the role of feeding performance in the evolution of facultative paedomorphosis. The present study shows an advantage of the polyphenism: morphological specialization causes variation of foraging efficiency between morphs and consequently may allow differentiation of diets and of microhabitat use.

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Literature Cited

Amundsen, P.-A. 1988: Habitat and food segregation of two sympatric populations of whitefish (*Coregonus lavaretus* L. s.l.) in Stuurajavri, Northern Norway. *Nordic J. Freshw. Res.* 64, 67–73.

Arntzen, J. W., Smithson, A. & Oldham, R. S. 1999: Marking and tissue sampling effects on body condition and survival in the newt *Triturus cristatus*. *J. Herpetol.* 33, 567–576.

Chacornac, J. M. & Joly, P. 1985: Activité prédatrice du triton alpestre (*Triturus alpestris*) dans un lac alpin (2125 m, Alpes françaises). *Acta oecol.* 6, 93–103.

Collins, J. P. & Holomuzki, J. R. 1984: Intraspecific variation in diet within and between trophic morphs in larval tiger salamanders (*Ambystoma tigrinum nebulosum*). *Can. J. Zool.* 62, 168–174.

Day, R. W. & Quinn, G. P. B. 1989: Comparisons of treatments after an analysis of variance in ecology. *Ecol. Monogr.* 59, 433–463.

Denoël, M. 2002: Paedomorphosis in the Alpine newt (*Triturus alpestris*): decoupling behavioural and morphological change. *Behav. Ecol. Sociobiol.* 52, 394–399.

Denoël, M. & Joly, P. 2000: Neoteny and progenesis as two heterochronic processes involved in paedomorphosis in *Triturus alpestris* (Amphibia: Caudata). *Proc. R. Soc. Lond. Ser. B, Biol. Sci.* 267, 1481–1485.

Denoël, M. & Joly, P. 2001: Adaptive significance of facultative paedomorphosis in *Triturus alpestris* (Amphibia, Caudata): resource partitioning in an alpine lake. *Freshw. Biol.* 46, 1387–1396.

Denoël, M., Duguët, R., Dzukic, G., Kalezić, M. & Mazzotti, S. 2001a: Biogeography and ecology of paedomorphosis in *Triturus alpestris* (Amphibia, Caudata). *J. Biogeogr.* 28, 1271–1280.

Denoël, M., Poncin, P. & Ruwet, J. C. 2001b: Sexual compatibility between two heterochronic morphs in the Alpine newt, *Triturus alpestris*. *Anim. Behav.* 62, 559–566.

Denoël, M., Hervant, F., Schabetsberger, R. & Joly, P. 2002: Short- and long-term advantages of an alternative ontogenetic pathway. *Biol. J. Linn. Soc.* 77, 105–112.

Hindar, K. & Jonsson, B. 1982: Habitat and food segregation of dwarf and normal arctic charr (*Salvelinus alpinus*) from Vansvatnet Lake, Western Norway. *Can. J. Fish. Aquat. Sci.* 39, 1030–1045.

Joly, P. 1981: Le comportement prédateur du triton alpestre (*Triturus alpestris*). I. Etude descriptive. *Biol. Behav.* 6, 339–355.

Joly, P. & Giacomini, C. 1992: Limitation of similarity and feeding habits in three syntopic species of newts (*Triturus*, Amphibia). *Ecography* 15, 401–411.

Lauder, G. V. & Reilly, S. M. 1988: Functional design of the feeding mechanism in salamanders: causal bases of ontogenetic changes in function. *J. Exp. Biol.* 134, 219–233.

Lauder, G. V. & Reilly, S. M. 1990: Metamorphosis of the feeding mechanism in tiger salamanders (*Ambystoma tigrinum*): the ontogeny of cranial muscle mass. *J. Zool.* 222, 59–74.

Lauder, G. V. & Reilly, S. M. 1994: Amphibian feeding behavior: comparative biomechanics and evolution (chap. 6). In: *Advances in Comparative and Environmental Physiology*, vol 18 (Bels, V., Chardon, M. & Vandewalle, P., eds). Springer-Verlag, Berlin, pp. 163–195.

Lauder, G. V. & Shaffer, H. B. 1993: Design of feeding systems in aquatic vertebrates: major patterns and their evolutionary interpretations. In: *The Skull*, vol. 3: Functional and Evolutionary Mechanisms (Hanken, J. & Hall, B. K., eds). Chicago Univ. Press, Chicago, pp. 113–149.

Lavin, P. A. & McPhail, J. D. 1986: Adaptive divergence of trophic phenotype among freshwater populations of the threespine stickleback (*Gasterosteus aculeatus*). *Can. J. Fish. Aquat. Sci.* 43, 2455–2463.

Liem, K. F. & Kaufman, L. S. 1984: Intraspecific macroevolution: functional biology of the polymorphic cichlid species *Cichlasoma minckleyi*. In: *Evolution in Fish Species Flocks* (Echelle, A. A. & Kornfield, I., eds). Univ. of Main Press, Orono, pp. 203–215.

Malmquist, H. J. 1992: Phenotypic-specific feeding behaviour of two arctic charr *Salvelinus alpinus* morphs. *Oecologia* 92, 354–361.

Malmquist, H. J., Snorrason, S. S., Skulason, S., Jonsson, B., Sandlund, O. T. & Jonasson, P. M. 1992: Diet differentiation in polymorphic Arctic charr in Thinvallavatn, Iceland. *J. Anim. Ecol.* 61, 21–35.

Meyer, A. 1989: Cost of morphological specialization: feeding performance of the two morphs in the trophically polymorphic cichlid fish, *Cichlasoma citrinellum*. *Oecologia* 80, 431–436.

Meyer, A. 1990: Ecological and evolutionary consequences of the trophic polymorphism in *Cichlasoma citrinellum* (Pisces: Cichlidae). *Biol. J. Linn. Soc.* 39, 279–299.

Reilly, S. M. & Lauder, G. V. 1988: Ontogeny of aquatic feeding performance in the Eastern newt, *Notophthalmus viridescens* (Salamandridae). *Copeia* 1988, 87–91.

Robinson, B. W. 2000: Trade offs in habitat-specific foraging efficiency and the nascent adaptive divergence of sticklebacks in lakes. *Behaviour* 137, 865–888.

Semlitsch, R. D. & Wilbur, H. M. 1989: Artificial selection for paedomorphosis in the salamander *Ambystoma talpoideum*. *Evolution* 43, 105–112.

Skulason, S. & Smith, T. B. 1995: Resource polymorphisms in vertebrates. *Trends Ecol. Evol.* 10, 366–370.

Smith, T. B. 1990: Resource use by bill morphs of an African finch: evidence for intraspecific competition. *Ecology* 71, 1246–1257.

Smith, T. B. & Skulason, S. 1996: Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annu. Rev. Ecol. Syst.* 27, 111–133.

Sokal, R. R. & Rohlf, F. J. 1995: *Biometry*. Freeman and Co, New York.

Statsoft-France. 2000: *Statistica pour Windows* (computer program manual). Maisons-Alfort.

Twitty, V. C. 1966: *Of Scientists and Salamanders*. Freeman and Co, San Francisco.

Whiteman, H. H. 1994: Evolution of facultative paedomorphosis in salamanders. *Q. Rev. Biol.* 69, 205–221.

Whiteman, H. H., Wissinger, S. A. & Brown, W. S. 1996: Growth and foraging consequences of facultative paedomorphosis in the tiger salamander, *Ambystoma tigrinum nebulosum*. *Evol. Ecol.* 10, 433–446.

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