Adaptive significance of facultative paedomorphosis in *Triturus alpestris* (Amphibia, Caudata): resource partitioning in an alpine lake

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Abstract

1. Facultative paedomorphosis is a polymorphism that has important evolutionary implications in promoting morphological differentiation and variation in habitat use. It occurs in several urodele species throughout the world. Several hypotheses based on life-history theory have been proposed to explain the wide range of habitats in which facultative paedomorphosis occurs, suggesting multifactorial causes.

2. In harsh habitats, such as mountain lakes, paedomorphosis might promote niche partitioning between morphs. This hypothesis was tested by comparing micro-habitat use and diet of two coexisting morphs in an alpine lake.

3. Paedomorphs occupied all microhabitats in the lake while metamorphs occurred only along the shoreline or at the water surface. Paedomorphic newts were frequent in deep water, where they foraged mainly on plankton. Plankton was poorly exploited by metamorphic newts, which fed mainly on terrestrial insects. Difference between morphs in microhabitat use, and consequently in the diet, were consistent in both sexes and in juveniles.

4. In adults, the mass and energy value of stomach contents did not differ between morphs, suggesting a similar food availability in the habitats occupied.

5. This study indicates habitat partitioning between morphs involving dietary differences. Specific benefits and costs of each ontogenetic pathway may allow their coexistence in this deep and fishless lake. Paedomorphosis benefits individual newts by making new food resources available and presumably reducing competition at the shore of the lake. However, the proximate causes of such an ontogenetic switch remain unclear.

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Introduction

Environment can interact with ontogenetic processes to determine phenotype variation through phenotypic plasticity (Scheiner, 1993). Such interactions can lead to discrete morphs, when developmental variation is canalized into qualitative alternatives (West-Eberhard, 1989; Whiteman, 1994; Voss & Shaffer, 1997). Current theories assume that the coexistence of different ontogenetic pathways in a population is the consequence of the selective pressures that result from the variability of ecological conditions when resources are spatially and temporally unpredictable (West-Eberhard, 1989; Semlitsch, Harris & Wilbur, 1990; Kaplan, 1992; Schlichting & Pigliucci, 1995). In such a context, the organism can take advantage of alternative ontogenetic pathways that can respond to reliable information on the future environment, or represent a bet-hedging strategy when such reliable information is not available (Seger & Brockmann, 1987; Scheiner, 1993). An evolutionary consequence of phenotypic plasticity is that phenotypic variation offers new targets to natural selection that can result in population differentiation and speciation.

Polymorphism includes alternative behavioural tactics (Gross, 1996), trophic morphs in amphibians (Maret & Collins, 1997), fishes (Meyer, 1990) and birds (Smith, 1990), castes in colonial insects (Harvell, 1994), wing dimorphism in insects (Roff, 1986) and shell dimorphism in barnacles (Lively, 1986). The temporal course of development, such as prolonged diapause in insects (Menu & Debouzie, 1995) and facultative paedomorphosis in urodeles (Whiteman, 1994; Denoël & Joly, 2000), is also a target of selection by variable environments.

In amphibians, larval habitats are often ecotones where ecological conditions such as water period,

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resource availability and predator density are highly variable and unpredictable (Joly & Morand, 1996). As a consequence, phenotypic plasticity is a common trait shared by both anurans (Wilbur & Collins, 1973; Newman, 1989; Morand, Joly & Grolet, 1997) and urodeles (Whiteman, 1994). Phenotypic plasticity is expressed through variation in the length of the larval period (Newman, 1989; Denver, Mirhadi & Phillips, 1998), morphology (Pfennig, 1992; Van Buskirk & Relyea, 1998) or age at maturity (Ryan & Semlitsch, 1998). In some populations of tailed amphibians, some of the larvae metamorphose before reaching sexual maturity, while others retain gills and gill slits, and mature under water as paedomorphic individuals. This trait is known as facultative paedomorphosis (Semlitsch, 1987; Whiteman, 1994; Ryan & Semlitsch, 1998). Such a heterochronic pattern, or change in the rate or timing of developmental events, is suspected to play an important role in both micro- and macroevolutionary processes (Gould, 1977; McKinney & McNamara, 1991; McNamara, 1997). In addition to amphibians (Wilbur & Collins, 1973), heterochronies are observed in mammals (Hafner & Hafner, 1984), birds (Livezey, 1992), fishes (Meyer, 1987) and invertebrates (Anstey, 1987).

The proportion of paedomorphic and metamorphic individuals varies among populations (Breuil, 1986; Semlitsch *et al.*, 1990; Whiteman, 1994). Experimental studies have investigated the mechanisms (i.e. density, pond drying, predation, temperature and lighting) that modulate the expression of paedomorphosis (Svob, 1965; Harris, 1987; Semlitsch, 1987; Semlitsch & Wilbur, 1989; Semlitsch *et al.*, 1990; Jackson & Semlitsch, 1993). Cross-breeding experiments and selection against metamorphosis can modify the occurrence of this trait in progeny, suggesting that plasticity also depends on genetic background (Tompkins, 1978; Semlitsch & Wilbur, 1989; Harris *et al.*, 1990; Semlitsch *et al.*, 1990; Voss, 1995; Voss & Shaffer, 1997). However, the fitness consequences of alternative tactics (paedomorphosis versus metamorphosis) remain poorly documented. Differences between morphs in prey size selection (Fasola & Canova, 1992; Fasola, 1993), habitat selection (Whiteman, Wissinger & Brown, 1996), rate of prey capture (Reilly & Lauder, 1988; Whiteman *et al.*, 1996), date of mating (Krenz & Sever, 1995), age at maturity (Ryan & Semlitsch, 1998; Denoël & Joly, 2000), and occurrence of breeding events (Whiteman, 1997) can contribute to the maintenance of paedomorphosis in newts and salamanders. From these observations and experiments, Whiteman (1994) proposed a theoretical framework by formulating alternative hypotheses to explain the occurrence of facultative paedomorphosis in contrasting environments. He suggested that paedomorphosis can be adaptive when conditions are favourable (high growth rate) by enabling reproduction at an earlier age than in metamorphosed individuals. In contrast, paedomorphosis can also prove adaptive under harsh conditions (low growth rate) given the cost of metamorphosis ('best-of-a-bad-lot' hypothesis: Whiteman, 1994). However, other factors such as habitat structure and biotic relationships are also suspected to influence the outcome of developmental pathways, through niche partitioning between the two forms.

Our aim was to examine the hypothesis of resource partitioning between the two forms. To this end, we compared feeding habits and habitat use between paedomorphs and metamorphs of the Alpine newt *Triturus alpestris* (Laurenti, 1768) in a population inhabiting a deep alpine lake.

Methods

Study site and species

La Cabane Lake (altitude 1950 m) is located in the southern French Alps (Long. 44°24' N, Lat. 6°24' E). In this lake, water level varies drastically during the year. In June 1997, maximum depth was 7 m and the lake area was approximately 1 ha. In August, drying up split the lake into two parts (1 and 5 m deep, respectively). In October, only the deepest part contained water, which was 2 m deep. Lake substratum consisted of rocks and sediment, but riparian and floating vegetation was absent.

The Alpine newt (*Triturus alpestris*) population was composed of adult metamorphs and paedomorphs, and of branchiate and metamorphosed juveniles. In this population, both morphs reach sexual maturity at the same age (Denoël & Joly, 2000). Adulthood was defined by the presence of well-developed cloaca, and the sex of individuals was determined using secondary sexual characters (e.g. dorsal crest, colour, shape of the cloaca). An individual was considered to be a branchiate juvenile or a paedomorph when the gill slits were open. Juveniles were considered branchiate when the gill slits were open and snout-vent length exceeded the usual size attained at metamorphosis in the study population (30 mm).

Sampling and analyses

Newts were sampled using a landing net from the shore, from a boat, or by scuba diving. Sampling effort was distributed according to a (date × microhabitat × time of day) design. Four microhabitats were sampled: shore (0–1 m depth), deep bottom (3–7 m depth), water column, and water surface. During each sampling session, the whole area of each habitat was sampled three times, at dawn, during midday and in the evening. This procedure was repeated three times, in June, August and October 1997. It allowed the determination of the proportion of paedomorphs in the population. Stomach contents of a random fraction of these animals were then collected using a gut-flushing procedure performed on anaesthetized animals (Joly, 1987), just after the newts were collected to avoid digestion (Schabetsberger, 1994). Sampled newts were measured (snout-vent length to the nearest mm) and weighed (to the nearest 0.1 g). All newts were released after gut flushing.

Stomach content of individuals were stored separately in 4% formaldehyde. Prey were identified and measured (total length) on squared paper under a stereoscopic microscope. Wet weight of ingested prey was estimated using a relationship between biomass and body length for each prey type (i.e. regression or specific weight for each prey size). They were established either by weighing fresh prey of different sizes or obtained from the literature (Jorgensen, 1979). In order to express stomach content mass independent of body size, we regressed it against newt snout-vent length. Biomass values were then converted to Joules using representative prey values given by Cummins & Wuycheck (1971) and Jorgensen (1979).

Statistical procedures

An ANOVA test with the *a posteriori* protected LSD test (Day & Quinn, 1989) was used to compare the number of ingested prey ('square root + 0.5' transformation) in morphs as well as the biomass and

energy values. A *t*-test was used for specific comparisons of diet in morphs within habitats where they coexist. A χ2 test for independent samples was also used to test the null hypothesis of both equal proportion of newts from the different categories among microhabitats and equal prey occurrence between each newt category (Siegel & Castellan, 1988; Statsoft France 2000).

Results

Population structure

The paedomorphs outnumbered the metamorphs, accounting for 79% of the adult population (n = 485) in the lake in June, 80% in August (n = 293) and 85% in October (n = 258). Percentages of metamorphs and paedomorphs were similar for males and females: 75 and 83% in June, 81 and 79% in August, and 74 and 87% in October, respectively. Among metamorphosed newts, the proportion of metamorphosed juveniles varied from 37% in June (n = 273) to 43% in August (n = 91), and 18% in October (n = 49).

Micro-habitat use

In each sampling period, we found paedomorphs and branchiate juveniles in all the microhabitats of the lake (i.e. along the shore, at water surface, in
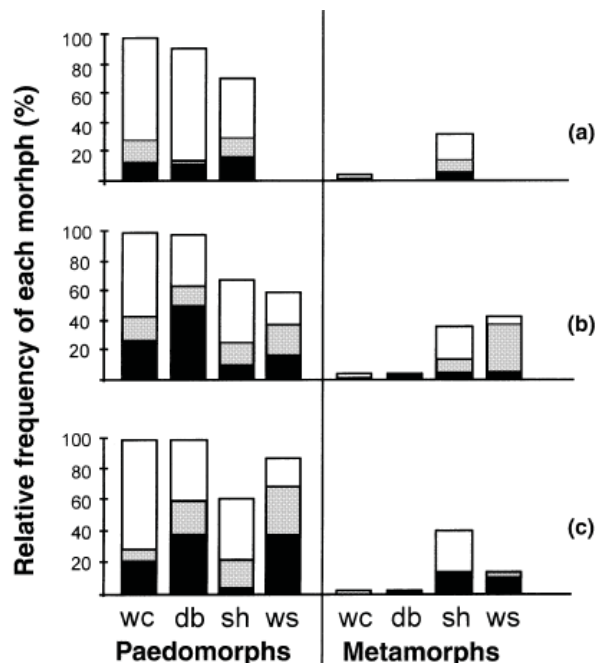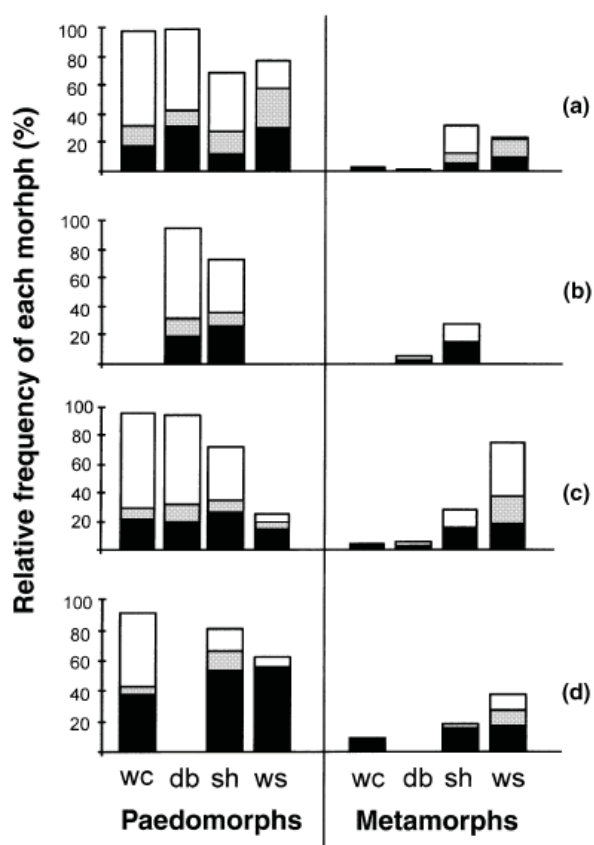

Figure 1. Spatial use of microhabitats in 1997. Each bar represents the proportion of newts of one of the two morphs in a given microhabitat (for a given microhabitat, the addition of the bar 'paedomorphs' and 'metamorphs' equals 100%). Black bars: females; shaded bars: males; white bars: juveniles. Wc: water column; db: deep bottom; sh: shore; ws: water surface. (a) June (wc: n = 238; dp: n = 159; sh: n = 463; ws: n = 57); (b) August, small basin (dp: n = 161; sh: n = 72); (c) August, large basin (wc: n = 168; dp: n = 89; sh: n = 72; ws: n=16); (d) October (wc: n = 89; sh: n = 60; ws: n = 79).

Figure 2. Daily use of microhabitats. Same legend as in Fig. 1. (a) dawn (wc: n = 101; db: n = 61; sh: n = 362); (b) mid-day (wc: n = 59; dp: n = 48; sh: n = 64; ws: n = 19); (c) dusk (wc: n = 78; db: n = 48; sh: n = 37; ws: n = 38).

the water column and on the bottom in deep water) whereas metamorphs and metamorphosed juveniles occupied limited habitats, mainly the shore and the water surface (June: χ2 = 186, d.f. = 15, P < 0.001; August – deep basin: χ2 = 117, d.f. = 15, P < 0.001; August – shallow basin: χ2 = 21, d.f. = 5, P = 0.01; October: χ2 = 186, d.f. = 10, P < 0.001; Fig. 1). Specific statistical comparisons between habitats and morphs were all significant (χ2, P < 0.05), except in October.

With regard to time of day, metamorphs were more abundant along the shore and at the water surface than in the water column or on the bottom on each sampling occasion (dawn: χ2 = 80, d.f.=10, P < 0.001; mid-day: χ2 = 73, d.f. = 15, P < 0.001; dusk: χ2 = 98, d.f. = 15, P < 0.001; Fig. 2). Specific statistical comparisons between habitats and morphs were all significant (χ2, P < 0.001).

Diet

We sampled 778 newt stomachs (378 in June, 218 in August and 182 in October), and identified 51 067 prey items. Overall, prey occurrence differed significantly in females (χ2 = 31.75, d.f. = 3, P < 0.001), males (χ2 = 26.47, d.f. = 3, P < 0.001) and juveniles (χ2 = 53.00, d.f. = 3, P < 0.001) of the two morphs (Fig. 3). Morph, gender and month of sampling, as well as their interactions, had a significant effect on the number of prey ingested (ANOVA, Table 1, Fig. 3).

Adult paedomorphs of each sex preyed significantly more on plankton than did adult metamorphs (*a posteriori* LSD test, P < 0.01, Fig. 3). Conversely, the metamorphs preyed more on terrestrial insects (LSD test, P < 0.001 for each sex, Fig. 3). Diets of males and females showed similar patterns. The same differences were found between branchiate and metamorphosed juveniles (Fig. 3).

Variation in the number of ingested prey between morphs was observed at the different sampling sessions (Table 2), except for fairy shrimps *Chirocepha-*
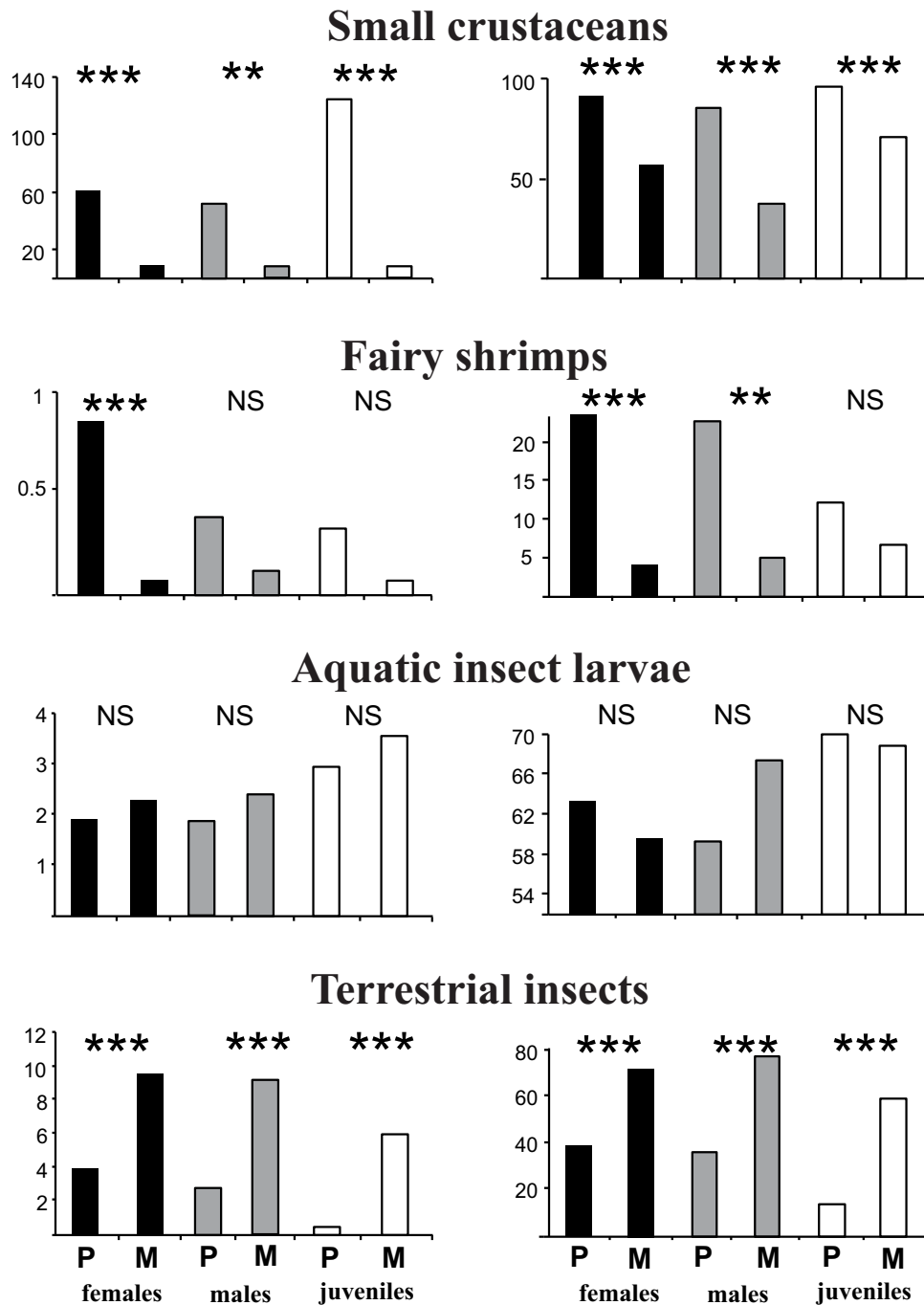
Small crustaceans

Fairy shrimps

Aquatic insect larvae

Terrestrial insects

Figure 3. Stomach contents. Left: mean prey numbers per stomach. Right: occurrence of each prey (proportion of stomachs containing each prey type). (a) small crustaceans (Cladocerans, Copepods, Ostracods); (b) fairy shrimps *Chirocephalus*; (c) aquatic insects (mainly larvae); (d) terrestrial insects. M: metamorphs; P: paedomorphs; NS: not significant difference between M and P; **$P < 0.01$; ***$P < 0.001$ (prey number: *a posteriori* protected LSD test; occurrence: χ^2 test).

lus in August and October, and terrestrial insects in August. However, the scarcity of these prey taxa at these dates prevented any firm conclusion concerning newt selectivity for them.

Differences in diet between morphs were less marked when particular microhabitats were considered. However, paedomorphs exhibited a greater preference than metamorphs for fairy shrimps along the shore in June ($P < 0.05$, *t*-test), for small crustaceans along the shore in June ($P < 0.01$, *t*-test), August ($P < 0.05$, *t*-test) and October ($P < 0.01$, *t*-test) and at water surface in October ($P < 0.05$, *t*-test), whereas metamorphs preyed more on terrestrial invertebrates than paedomorphs at the shoreline in June ($P < 0.05$, *t*-test).

Prey mass and energetic gain analyses

Morph had a significant effect on the biomass of gut content (regressed on body length) ($F_{1,772} = 7.052$, $P < 0.01$), but not gender ($F_{2,772} = 0.135$, $P = 0.87$) nor their interaction ($F_{2,772} = 1.721$, $P = 0.18$). Biomass of gut contents was greater in branchiate juveniles than in metamorphosed juveniles (LSD test, $P < 0.01$), but not in adult newts (LSD test) (Fig. 4).

Neither morph ($F_{1,772} = 0.433$, $P = 0.51$), nor gender ($F_{2,772} = 0.602$, $P = 0.55$) or their interaction ($F_{2,772} = 1.115$, $P = 0.32$) had an effect on the energy content of the gut (regressed on body length) (Fig. 4).

Table 1. Multivariate analysis of variance on the relative abundance of prey

Source	Wilk's λ	df	F	P
morph	0.844	4,757	35.010	<0.0001
gender	0.968	8,1514	3.110	<0.01
month	0.827	8,1514	18.920	<0.0001
morph × gender	0.977	8,1514	2.261	<0.05
morph × month	0.919	8,1514	8.111	<0.001
gender × month	0.968	8,1514	3.110	<0.05
morph × gender × month	0.945	16,231	2.708	<0.001

Figure 4. Mean (± SE) prey biomass (mg) and mean energetical equivalent (J) of stomach contents, weighted by newt snout-vent length (mm). M: metamorphs; P: paedomorphs. ***$P < 0.001$ (t-test). The other differences between M and P were non-significant.

Discussion

We detected substantial differences in habitat use between the morphs. Paedomorphic newts occupied all microhabitats in the lake (shore, bottom in deep water, water column, and water surface), while metamorphic newts mainly occupied the shore and the water surface. Branchiate juveniles were also present in all microhabitats of the lake, although metamorphosed juveniles were mainly present close to the shore.

Overall, variation in diet between paedomorphs and metamorphs was consistent with variation in habitat use, paedomorphs preying more on plankton (fairy shrimps and smaller crustaceans) and less on terrestrial insects than metamorphs. Density of terrestrial insects is expected to be close to zero in the water column where paedomorphs preferentially foraged, although insects that fell on the lake surface were more profitable than plankton to metamorphs along the shore and at the water surface. At depths where metamorphs became scarce, paedomorphs took planktonic prey. However, paedomorphs were also found foraging together with metamorphs along the shore or at the water surface. At the water surface, newts of each morph waited for prey using a characteristic floating behaviour previously described by Chacornac & Joly (1985) and Joly & Giacoma (1992). If we consider the whole biomass of ingested prey or its energy equivalent, both tactics (i.e. those of metamorphs and paedomorphs) provided similar gains. Thus, foraging on a numerous but small planktonic prey can lead to similar stomach fullness as foraging on a few large insects. As metamorphs and paedomorphs were simultaneously present under water from thawing to freezing, temporal resource partitioning did not occur.

Skulason & Smith (1995) suggested that a relaxation of interspecific competition and the availability of vacant niches are essential to promote resource polymorphisms. Our data from La Cabane lake fits these predictions well. It is a heterogeneous habitat where Alpine newts are top predators and have no vertebrate competitors. Facultative paedomorphosis appears to be a trophic polymorphism that allows diet specializations among alternative morphs similar to those found in fishes (Hindar & Jonsson, 1982; Meyer, 1990; Malmquist et al., 1992; Ruzzante et al., 1998) and birds (Smith, 1990). It also allows numerous individuals to avoid a potential intraspecific competition in the littoral zone by occupying a vacant niche in deep water. Although cannibalism is frequent in some salamander species (Maret & Collins, 1997), it does not occur in the Alpine newt and thus cannot explain habitat differences.

The hierarchy in resource partitioning shown here fits Shoener's rule (1974), which asserts that partitioning is more frequent along the habitat axis than along the food axis, and that temporal partitioning is rare. Habitat mainly acts through its heterogeneity (Smith & Skulason, 1996) along a depth gradient in La Cabane lake. In this context, the persistence of metamorphs may be related to specific advantages such as the avoidance of crowding during partial lake drying, niche enlargement through exploitation of terrestrial habitats, and avoidance of inbreeding by colonizing other aquatic sites.

Table 2. Significant differences in the number of ingested prey in female paedomorphs and metamorphs, male paedomorphs and metamorphs, and branchiate and metamorphosed juveniles in each of the three sampling periods (*a posteriori* protected LSD test)

	Females			Males			Juveniles		
	June	August	October	June	August	October	June	August	October
Prey taxa n newts									
B	102	69	81	72	34	17	115	65	40
M	27	19	23	22	7	11	40	24	10
Small crustaceans		***	*		*		***	***	***
Chirocephalus	***						**		
Aquatic insects larvae							***	**	
Terrestrial insects	***		***	***		*	***		***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Grey area refer to a preponderance of the prey in the branchiate newts.
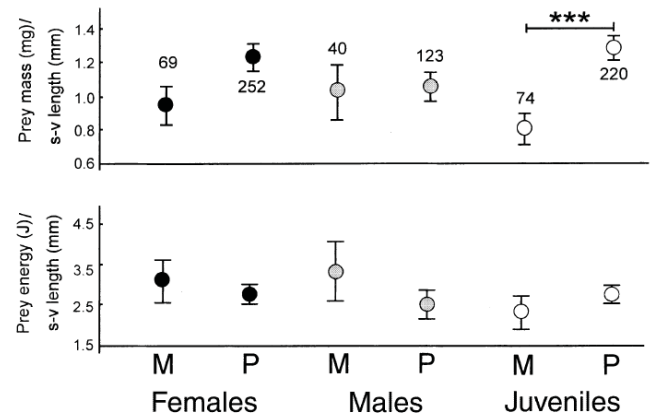B: branchiate newts, M: metamorphosed newts.

The outnumbering of metamorphs by paedomorphs observed across years (Breuil, 1986; this study) suggests that more larvae become mature instead of metamorphosing as more space and food are available for paedomorphs.

The diet of trophic morphs have been shown to be more similar when resources are abundant (Hindar & Jonsson, 1982; Smith, 1990). However, in La Cabane lake, the diet of the two morphs differed at all times of the year. Similarly, Malmquist *et al.* (1992) observed continuous segregation in Arctic charr. They suggested that ecological stability, heterogeneity of niches and low fish species diversity were all relevant features promoting morphological specialization. The characteristics of La Cabane lake and its biological community fit these criteria well, as the lake contains a large volume of water and incorporates several microhabitats and inhabited by only one vertebrate species.

Some experimental studies have shown that paedomorphosis may be promoted in permanent waters, at low density and in the absence of predators or competitors (i.e. fish) (Harris, 1987; Semlitsch, 1987; Semlitsch & Wilbur, 1989; Semlitsch *et al.*, 1990; Jackson & Semlitsch, 1993). Considering ultimate causes, Whiteman (1994) and Ryan & Semlitsch (1998) pinpointed the importance of fitness consequences of each ontogenetic alternative. Fitness differences between morphs have been demonstrated by several laboratory and field experiments (Reilly & Lauder, 1988; Krenz & Sever, 1995; Whiteman *et al.*, 1996; Whiteman, 1997; Ryan & Semlitsch, 1998; Denoël & Joly, 2000). In the population we studied, the age structure of the two morphs was similar and sexual maturation was similarly delayed in the two morphs by low temperature (Denoël & Joly, 2000). Moreover, we found no evidence of significant variation in energy intake between the two morphs. In demonstrating clear niche partitioning between the morphs, our study highlights the benefits that can be gathered by paedomorphs in exploiting resources in deep water and presumably avoiding competition at the shore.

Persistence of facultative paedomorphosis may be permitted by a trade-off between the two tactics (metamorphosis versus paedomorphosis), as suggested to account for shell dimorphism in a barnacle (Lively, 1986). Such a polymorphism has already been shown to allow individuals in a population to cope better with local variation in prey availability (Meyer, 1990; Maret & Collins, 1994, 1997). Moreover, facultative paedomorphosis is a reversible trait that allows newts to switch to the other morph when the local environment deteriorates (presence of fish, crowding and drying: Harris, 1987; Semlitsch, 1987; Jackson & Semlitsch, 1993). However, the proximate causes of the ontogenetic switch remain unclear. Density and growth rates in the larval stage are usual candidates for orienting ontogenetic pathways. Our present knowledge of the Alpine newt population of La Cabane Lake neither supports the paedomorphic advantage hypothesis (earlier age at maturity by delaying metamorphosis) nor the best-of-a-bad-lot hypothesis (lower larval growth rate). Identification of how environmental information influences switching from the metamorphic to the paedomorphic pathway remains a challenge for further investigations.

Acknowledgments

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