

# Size-related predation reduces intramorph competition in paedomorphic Alpine newts

Mathieu Denoël and Pierre Joly

**Abstract:** Evolutionary theory assumes that facultative paedomorphosis in newts and salamanders is adaptive in allowing either a younger age at maturity or resource partitioning between the heterochronic morphs. In newt populations that only take the metamorphic ontogenetic pathway, juveniles are terrestrial and avoid food competition with larvae and breeding adults. In contrast, in populations where paedomorphosis occurs, branchiate newts of all sizes coexist in the aquatic habitats, posing the question of whether intramorph competition exists and its relationship with the evolution of paedomorphosis. We studied size-related predation in such a size-structured community of branchiate Alpine newts (*Triturus alpestris*) inhabiting a deep alpine lake. Although gape limitation may explain such size-related predation, individuals also exhibited selectivity according to prey size. Amongst small prey that were within the capture range of all newt size classes, smaller newts preyed on smaller items than did larger ones. We assume that such decisions favour the coexistence of different-sized individuals. It is suspected that such size-selective predation on items which are avoided by water-living metamorphs allows the maintenance of facultative paedomorphosis, in favouring resource partitioning between morphs.

**Résumé :** Chez les tritons et les salamandres, les théories évolutives considèrent que la pédomorphose facultative est adaptative en permettant l'acquisition précoce de la maturité sexuelle ou le partage des ressources entre les formes hétérochroniques. Dans les populations strictement métamorphiques, les juvéniles sont terrestres et évitent de ce fait toute compétition pour la nourriture avec les larves et les adultes reproducteurs. Au contraire, au sein des populations pédomorphiques, des tritons branchiés de différentes tailles coexistent dans l'habitat aquatique. Cette situation soulève le problème de la compétition intramorphique et de sa relation avec la pédomorphose. Nous avons étudié la prédation en fonction de la taille dans une telle communauté structurée par la taille de tritons alpestres (*Triturus alpestris*) branchiés dans un lac alpin profond. Bien que la capacité limitée d'ouverture de la bouche puisse contribuer à la sélectivité en fonction de la taille des prédateurs, cette sélectivité est également reliée à la taille des proies. Parmi les proies de tailles accessibles à toutes les classes de taille de tritons, les petits tritons consomment de plus petites proies que les grands tritons. Si les causes immédiates de telles règles de décision demeurent inconnues, nous considérons que cette sélectivité assure la coexistence d'individus de tailles différentes. Une telle sélection reliée à la taille et exercée sur les proies peu utilisées par les formes métamorphiques aquatiques permet sans doute le maintien de la pédomorphose facultative en favorisant le partage des ressources entre les différents morphes.

## Introduction

Resource partitioning is known to reduce competition between coexisting species and thus allows their coexistence within the same habitats (Tokeshi 1999). Space, diet, and time are all resources that can be used differently by coexisting species (Schoener 1974; Joly and Giacoma 1992). Numerous species are polymorphic, with different morphs coexisting in the same environment (Skulason and Smith 1995; Smith and Skulason 1996). The alternative morphs can coexist because of differential use of habitat or feeding resources. Such differences in resource use can be promoted by differences in morphology (Sage and Selander 1975; Lavin and McPhail

1986; Meyer 1990; Smith 1990; Collins et al. 1993; Ruzzante et al. 1998).

Facultative paedomorphosis is a heterochronic polymorphism that implies the retention of juvenile characters in the adult (Gould 1977; Semlitsch and Wilbur 1989). Paedomorphic individuals may have the advantage of avoiding the cost of metamorphosis, allowing them to reach sexual maturity at a younger age or to experience other fitness benefits (the "paedomorph advantage" hypothesis; Whiteman 1994; Ryan and Semlitsch 1998). In contrast, in harsh habitats paedomorphosis may result from an incapacity to reach metamorphosis because of reduced growth rates (the "best-of-a-bad-lot" hypothesis; Whiteman 1994). Paedomorphs and metamorphs appear to use aquatic habitats differently (Whiteman et al. 1996). In the aquatic habitats where they live syntopically, the two heterochronic morphs also appear to use different resources (Fasola and Canova 1992; Fasola 1993; Denoël and Joly 2001).

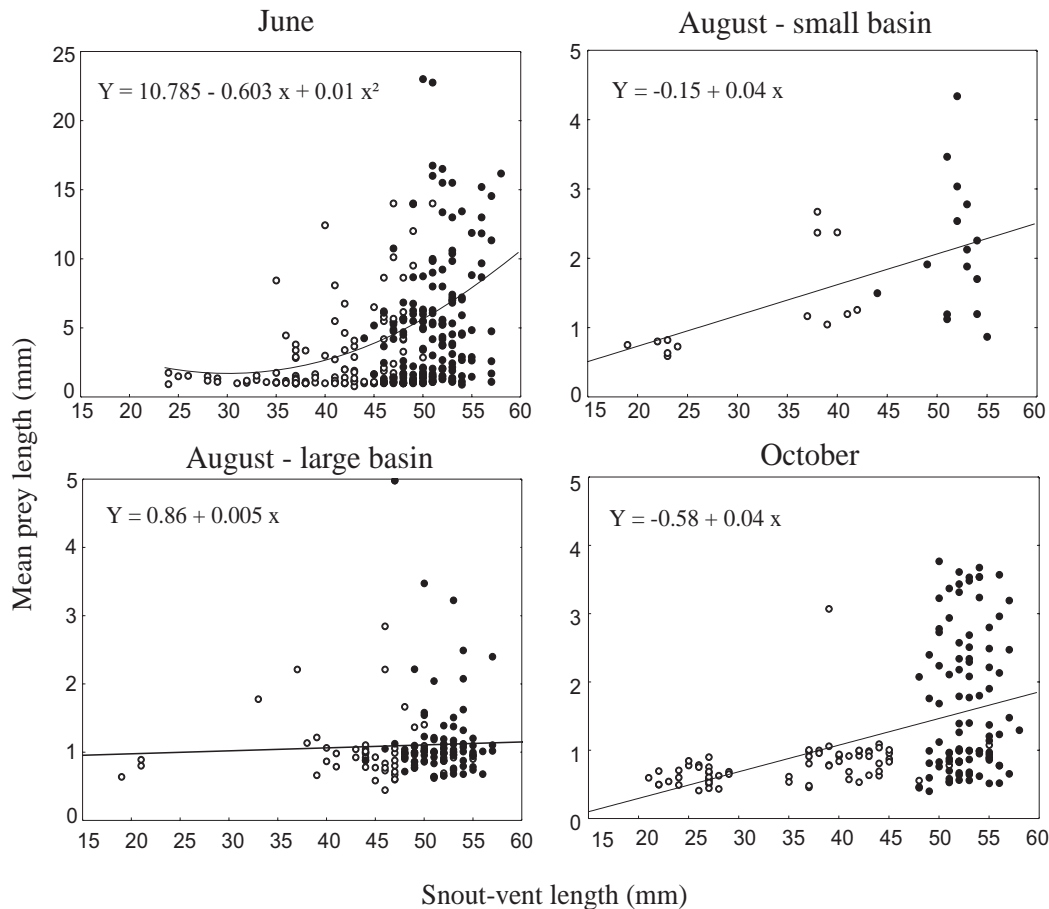
A consequence of taking the paedomorphic ontogenetic pathway is that newts or salamanders are constrained to occupy the same aquatic site as long as metamorphosis does not occur. In the aquatic environment, both habitat and food partitioning can weaken intermorph competition (Denoël

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**Fig. 1.** Regressions between snout–vent lengths of branchiate Alpine newts (*Triturus alpestris*) and mean prey lengths in June, August (small and large lake basins), and October. ○, immature newts; ●, adult newts.



and July 2001). Paedomorphic newts occupy deeper habitats (water column, deep bottom) than do metamorphic newts. In such deep habitats their diet is less diversified than that of metamorphs, as it is mainly composed of planktonic prey (Denoël and Joly 2001). As a consequence, competition among branchiate individuals could arise from similar use of resources. Moreover, as maturation of Alpine newts requires 4–5 years in such harsh habitats (Denoël and Joly 2000), a large number of different-sized branchiate individuals (larvae, juveniles, and adult paedomorphs) have to coexist in the same lake, posing the question of whether there is resource partitioning among them.

Variation in body size can favour niche segregation (Hutchinson 1959). Indeed, within a urodele population, different-sized individuals have been shown to select prey according to their size (Leff and Bachmann 1986; Kuzmin 1991; Joly and Giacoma 1992; Magalhaes 1993), although this is not always the case (Galbraith 1967; Petranksa 1984). Both prey availability (Werner and Hall 1974; Smith and Petranksa 1987) and gape limitation (Smith and Petranksa 1987; Webb and Shine 1993) are factors that can affect size relationships between prey and predators, while optimal foraging tactics may maximize feeding gains by allowing selection of prey of a particular size (Nuutinen and Ranta 1986; Rincón and Lobón-Cerviá 1999).

Our aim was to test the hypothesis of assortative size foraging in immature and adult branchiate newts. Such size-

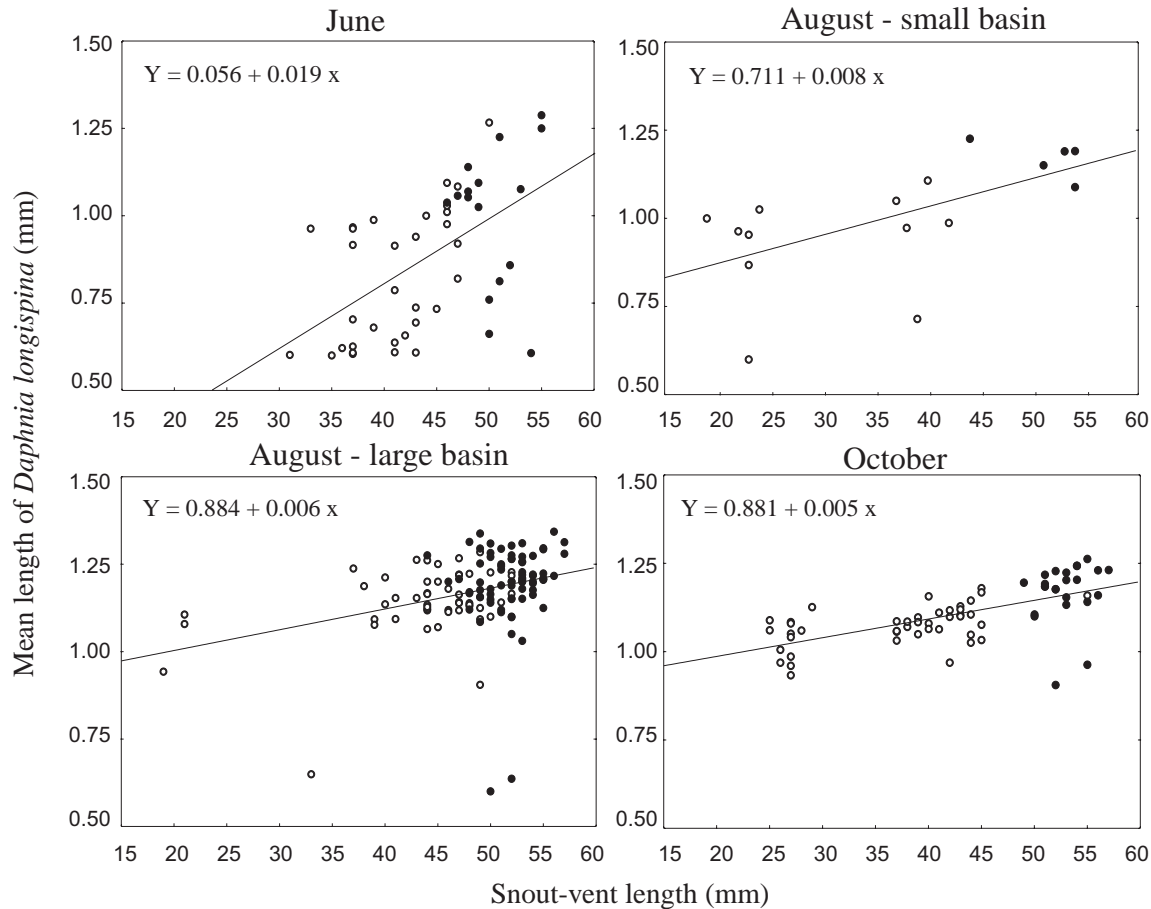
related selectivity is assumed to lower intramorphic competition and favour the maintenance of paedomorphosis, as such a process contributes to habitat partitioning between morphs in a habitat devoid of other competitors (Denoël and Joly 2001). To this end, we analysed prey sizes and prey types in the diet of different-sized branchiate newts sampled in an alpine lake during several sampling periods.

## Material and method

The study site was Lac de la Cabane (1950 m elevation) in the French Alps (UTM coordinates 32TKQ91). Maximum depth was 7 m and area approximately 1 ha. The lake substratum was composed of rocks and sediment with no riparian or floating vegetation. Water level was maximal in June but decreased during summer and autumn. As the water level decreased, the lake split into two basins in August. One basin was deeper than the other. In October, only the deeper basin still retained water.

The Alpine newt (*Triturus alpestris*) population of this lake is composed of both paedomorphic and metamorphic individuals. Adult paedomorphic newts retain larval attributes (i.e., gills and gill slits) while being sexually active. In contrast, maturation occurs several years after metamorphosis in metamorphic newts. In the studied population, both forms require 4–5 years to reach maturity (Denoël and Joly 2000). As a consequence, immature branchiate newts from 0+ to 3–4 years old coexist with adult branchiate newts from different cohorts, leading to a size-structured population. We studied immature branchiate newts when their size exceeded 19 mm. Whereas metamorphic newts only occupied riparian and water-

**Fig. 2.** Regressions between snout–vent lengths of branchiate Alpine newts and mean lengths of ingested *Daphnia longispina* in June, August (small and large lake basins), and October. ○, immature newts; ●, adult newts.



surface microhabitats, branchiate newts occurred in all microhabitats in the lake down to 7 m depth (Denoël and Joly 2001).

Branchiate newts were sampled in June, August, and October 1997 using a landing net from a boat or by scuba diving to sample all microhabitats in the lake. In August, the shallow and the deep basins were sampled separately. Stomach contents were collected following either a gut-flushing procedure performed on anaesthetized animals (Joly 1987) or, for the smallest individuals, following a dissection. With respect to gastric evacuation rates (Schabetsberger 1994), the guts were flushed just after the newts were collected. Snout–vent lengths were measured (in millimetres). All the newts were released thereafter.

Stomach contents were stored individually in 4% formaldehyde. Six prey taxa were identified: *Daphnia longispina*, *Chydorus sphaericus* Copepoda, *Chirocephalus diaphanus* aquatic insects, and terrestrial insects). Prey were ranked according to 1-mm length classes except for *D. longispina* for which we used 0.4-mm classes. For each newt, mean prey lengths were used to avoid pseudo-replication in the analyses. To study size selection on *D. longispina*, only stomach samples with more than 25 items were taken into account, to avoid any bias due to stomachs containing low numbers of water fleas.

Regressions were fitted (Zar 1996) between mean prey lengths and newt snout–vent lengths. The best model was selected on the basis of the lowest Akaike Information Criterion, i.e., an arithmetic function of the deviance and the number of parameters estimated (Sakamoto et al. 1986). Spearman's correlation coefficients ( $r_s$ ) between prey lengths and newt lengths were tested by  $t$  tests. Newts were ordered among three equally broad size classes (19–32, 33–46, 47–60 mm). A Kruskal–Wallis  $H$  test was used to test

the null hypothesis that the three newt size classes did not differ in numbers of ingested prey (Siegel and Castellan 1988).

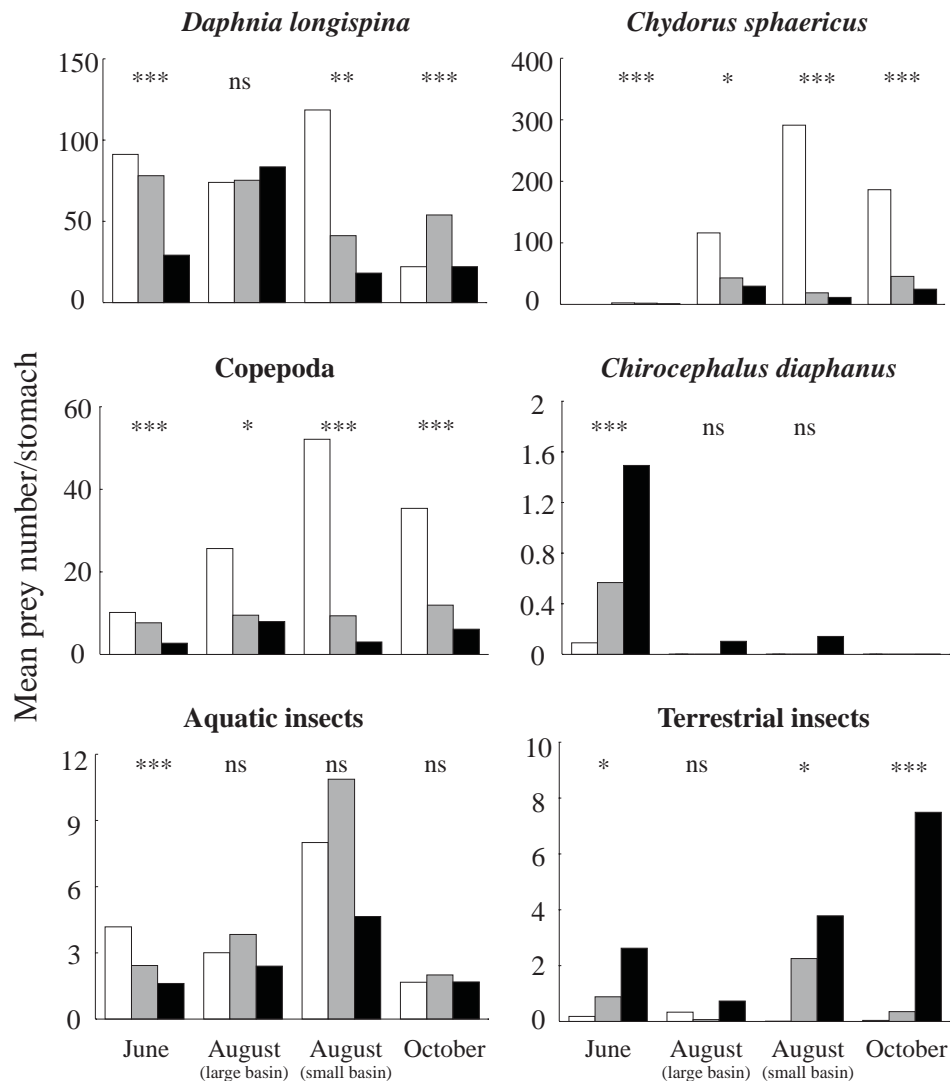
## Results

We sampled 639 branchiate newts (252 paedomorphic females, 123 paedomorphic males, and 264 immature branchiate individuals). The samples were collected in June (297), August (149 from the large basin; 28 from the small basin), and October (165). They yielded 57562 identified prey items. The analysis of size-selective predation on *D. longispina* was based on 48 stomach contents in June, 124 from the deep basin in August, 16 from the shallow basin in August, and 67 in October (from the deep basin only).

Newt snout–vent lengths were positively correlated with lengths of ingested prey in June ( $r_s = 0.450$ ,  $t_{295} = 8.659$ ,  $P < 0.001$ ), those from the small basin in August ( $r_s = 0.534$ ,  $t_{26} = 3.224$ ,  $P < 0.01$ ), and those in October ( $r_s = 0.689$ ,  $t_{163} = 7.682$ ,  $P < 0.001$ ), but not those from the large basin in August ( $r_s = 0.135$ ,  $t_{147} = 1.656$ ,  $P = 0.10$ ) (Fig. 1). More precisely, as newts became larger, the range of prey sizes became broader by the addition of larger prey to a diet basically composed of small prey. The range of prey sizes was considerably larger in June (up to 25 mm) than during the other sampling sessions (up to 4–5 mm).

Newt snout–vent lengths were always positively correlated with lengths of ingested *D. longispina* (June:  $r_s = 0.575$ ,  $t_{46} =$

**Fig. 3.** Variation in the contribution of principal prey types to the diet of branchiate Alpine newts according to body size and date. Open bars denote 19–32 mm long newts (June:  $N = 11$ ; August, large basin:  $N = 3$ ; August, small basin:  $N = 6$ ; October:  $N = 27$ ); shaded bars denote 33–46 mm long newts (June:  $N = 95$ ; August, large basin:  $N = 31$ ; August, small basin:  $N = 8$ ; October:  $N = 37$ ); and solid bars denote 47–60 mm long newts (June:  $N = 191$ ; August, large basin:  $N = 115$ ; August, small basin:  $N = 14$ ; October:  $N = 101$ ). \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ; ns,  $P \geq 0.05$  (Kruskal–Wallis  $H$  test).



4.763,  $P < 0.001$ ; small basin in August:  $r_s = 0.712$ ,  $t_{14} = 3.788$ ,  $P < 0.01$ ; large basin in August:  $r_s = 0.372$ ,  $t_{122} = 4.425$ ,  $P < 0.001$ ; October:  $r_s = 0.689$ ,  $t_{65} = 7.668$ ,  $P < 0.001$  (Fig. 2).

The three newt size classes differed according to prey type and prey size in most of the samples (Fig. 3). The smaller newts ate more *D. longispina*, *C. sphaericus*, and Copepoda (prey from 0.3 to 2 mm long) than the larger ones. Conversely, the larger newts ate more *C. diaphanus* (from 10 to 20 mm long) and terrestrial insects (various sizes from a few millimetres to around 30 mm) than the smaller ones. These differences were significant in most samples (Fig. 3).

## Discussion

Size-related predation was found in the studied population of branchiate newts. Whereas the smallest newts preyed only on small prey close to 1 mm in length, the largest newts ate

both large and small prey. This pattern was detected in all samples. The nonsignificance of variation in the large-basin samples in August was possibly due to the scarcity of small newt larvae at that date. In June, large newts foraged on bigger prey than in other months, probably as a consequence of a high abundance of fairy shrimps (*C. diaphanus*) during that period (Figs. 1 and 3). Such size-related predation relied both on differences in prey-related selection (only large newts preyed regularly on fairy shrimps and terrestrial insects) and on size-related selection as demonstrated by the significant relationship between newt size and *D. longispina* size in their diet (Fig. 2).

The absence of large prey in the diet of small individuals was probably due to gape limitation, as mouth gape is proportional to body length. Catching large prey is probably impossible or very difficult for small newts, as their mouth does not open more than 3 mm. Nevertheless, mean prey size was generally smaller than the gape size of small (2–

3 mm) and medium-sized (3.5–5 mm) newts. The analysis of size-based selection on *D. longispina* also revealed the same trend as that observed when all prey were considered together. Correlations between *D. longispina* lengths and newt lengths were positive in all sampling periods. For such small prey, gape limitation cannot be considered a selective factor. Selectivity for large *D. longispina* could be explained by higher profitability of large prey despite probable longer searching times because the largest individuals are usually the rarest in planktonic communities (Ranta and Nuutinen 1985). However, the balance between gains from and costs of foraging relative to body size has never been precisely established in newts.

Evidence of size-related predation was obtained at each sampling occasion but with different modalities according to the date, probably because of variation in prey availability. Several authors have shown an effect of prey availability on prey selection (Werner and Hall 1974; Smith and Petranksa 1987). Although we did not precisely estimate variation in prey densities, we noted that some prey were rare early (*C. sphaericus*) or late (*C. diaphanus*) in the season or were occasional (terrestrial insects) depending on climatic conditions. Variation in the intensity of prey selection may be explained by such prey-density variation but requires laboratory experiments for confirmation. Variations in habitat structure during the course of lake drying and changes in newt density may also influence resource use by newts.

Because of habitat partitioning between morphs, paedomorphic newts mainly exploited the deeper parts of the lake (Denoël and Joly 2001), where they constituted a size-structured guild foraging mainly on plankton. Size-related predation was suspected to favour the coexistence of newts belonging to different size classes in the deeper parts of the lake. The subsequent reduction of intramorph competition may allow the paedomorphic newts to coexist with metamorphic newts, which predominated at the water surface and along the shore.

Because growth rates were low in the studied population (Denoël and Joly 2000), it is suspected that paedomorphosis may result from a “best-of-a-bad-lot” tactic: at the larval stage, an individual could benefit from delaying metamorphosis if its growth rate is low and the costs of metamorphosis impair winter survival (Whiteman 1994). Maintenance of facultative paedomorphosis in an alpine lake may be favoured by substantial resource partitioning that would allow broader use of resources in a habitat devoid of other vertebrate competitors. It has been suggested that this last condition favours trophic polymorphism (Skúlason and Smith 1995). In this way, facultative paedomorphosis is a specific tactic that allows each individual to do the best it can. As metamorphosed individuals ensure inbreeding avoidance by dispersing among ponds, paedomorphic individuals improve their fitness in exploiting resources that are out of range of metamorphs (Denoël 2001). Such adaptive intrapopulation niche partitioning is made possible by lowering intramorph competition through size-related predation.

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