

Habitat partitioning in facultatively paedomorphic populations of palmate newts *Triturus helveticus*

Mathieu Denoël

The life cycle of newts of the genus *Triturus* is characterized by an aquatic larval stage, followed by a succession of transitions between the aquatic and terrestrial habitats. Water remains essential because it is the place for reproduction (1). However, in some populations, the terrestrial component is eliminated. The larvae acquire sexual maturity before metamorphosis, and then retain their gills and gill slits. This alternative path of development is paedomorphosis. In most cases, only a part of the population follows the paedomorphic ontogenetic pathway, while the other part normally metamorphoses (facultative paedomorphosis) (2).

Habitat is an essential key in the persistence of facultative paedomorphosis in natural populations of newts and salamanders. Laboratory experiments have shown that more larvae become paedomorphic in permanent waters than in temporary waters (3). In drying ponds, larvae and paedomorphs are constrained either to die or to metamorphose into the terrestrial morph. However, when other aquatic habitats are in proximity, they can survive by migrating without losing their larval attributes (4). Heterogeneous habitats composed of permanent and temporary habitats are usually differently used by the two morphs. Both paedomorphs and metamorphs breed in permanent ponds, but only the metamorphs are able to use drying ponds to forage on transient energetic resources (5).

Heterogeneity acts also within a single aquatic habitat on the scale of microhabitats that differ by components such as water depth. Strong space partitioning has been observed in deep lakes, in which paedomorphs were abundant in the water column and metamorphs in benthic areas and at the water surface (2, 6). In more homogeneous ponds, although some partitioning existed, the two morphs largely used all available microhabitats (7). Because all these results were obtained in a single species (the Alpine newt *Triturus alpestris*), comparative studies on other model species are needed.

Paedomorphosis was observed not only in the Alpine newt, but also in the palmate newt *Triturus helveticus* (8). Most populations of *T. helveticus* are located in southern France and inhabit environments different from that of paedomorphic Alpine newts (8, 9). In this area, all the aquatic habitats of *T. helveticus* are manmade ponds surrounded by arid lands (limestone plateau). The aim of this study was to find out whether paedomorphic and metamorphic palmate newts use their aquatic habitat differently.

Newts were caught in two private cattle ponds, locally known as “lavagnes” of Southern Larzac

(Department of Hérault, France). One of the ponds is located at the north of Le Coulet village at an elevation of 580 m above sea level (43°49'N, 3°31'E). Surface area is 115 m² and depth 2 m. The other pond is within Canourgue farmland at Groupillers at an elevation of 695 m (44°41'N, 3°23'E). Surface area is 175 m² and depth 2.4 m. Collection took place in May 2003. Ponds were divided into two zones: shallow (0–2 m from the shore-line, 0–1 m depth) and deep (2–4 m from the shore-line, i.e. in the central zone of the pond, 1–2 m depth). Collecting protocol consisted in doing blind net sweeps in the pond in the two zones at the same time (two persons). All the areas of the ponds were sampled by following the outside circumference of the two areas and dipnetting approximately every 50 cm. Census stopped when numerous successive dipnetting did not result in any newts caught. Vegetation is abundant in the two zones, although a bit less developed at the center of the ponds. Results of the census are shown in Figure 1. Prey niche overlap between morphs was calculated using Schoener's index (10):

$$C = 1 - 0.5 \left(\sum_i |P_{xi} - P_{yi}| \right)$$

where p_{xi} is the proportional utilization of microhabitat type i by morph x , and p_{yi} the proportional utilization of microhabitat type i by morph y . The index ranges from 0 (no microhabitat in common) to 1 (two microhabitats in common). Chi-square tests in 2 x 2 contingency tables were computed to test for differences between morphs in microhabitat use. Differences in morph ratio and sex ratio were obtained by testing observed values against expected values (equal morph ratio and sex ratio, respectively) with chi-square tests.

At Coulet pond, metamorphs significantly outnumbered paedomorphs. Metamorphs represented 61% of the population ($\chi^2=16.89$, $n=342$, $P < 0.001$). 77% of the adults present in the shallow area were metamorphs. In the deep area, only 52% were metamorphs ($\chi^2 = 21.01$, $n = 342$, $P < 0.001$). Sex ratio was female-biased in paedomorphs (females = 74%; $\chi^2 = 29.84$, $n=133$, $P < 0.001$) and balanced in metamorphs (females=54%; $\chi^2=1.73$, $n=209$, $P = 0.19$). Contrary to paedomorphic females, paedomorphic males were very rare in shallow areas ($\chi^2 = 6.72$, $n = 77$, $P < 0.001$). No significant difference between sexes was found in the metamorphs. Niche overlap was 0.76. At Canourgue-Groupillers pond, metamorphs were significantly more nume-

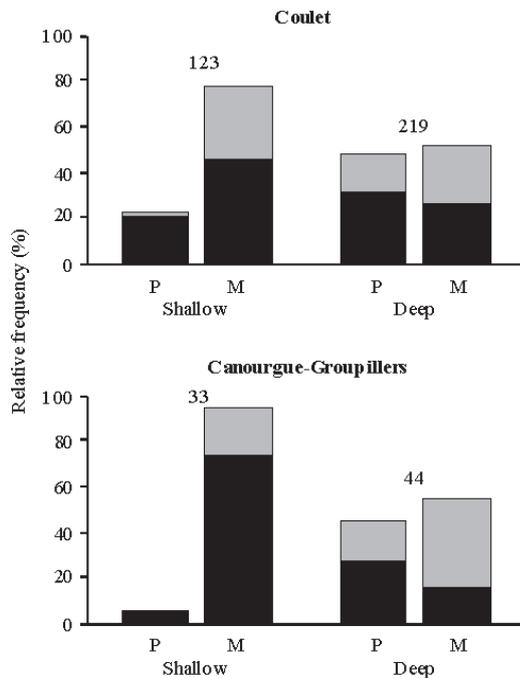


Figure 1. Spatial use of the shallow and deep microhabitats in Coulet and Canourgue-Groupilliers ponds (Larzac, France). P: paedomorphs, M: metamorphs; black bars: females, open bars: males.

rous than paedomorphs. They represented 71% of the population ($\chi^2 = 14.14$, $n = 77$, $P < 0.001$). 94% of the adults present in the shallow area were metamorphs. In the deep area, only 55% were metamorphs ($\chi^2 = 14.34$, $n = 77$, $P < 0.001$). Sex ratio was female-biased in paedomorphs (females = 71%; $\chi^2 = 5.14$, $n = 28$, $P < 0.05$) and balanced in metamorphs (females = 56%; $\chi^2 = 0.89$, $n = 55$, $P = 0.35$). The low number of individuals present in the shallow area did not allow microhabitat comparisons for paedomorphs. In metamorphs, sex ratio was different in the shallow area (78% of females) and the deep area (29% of females) ($\chi^2 = 12.81$, $n = 209$, $P < 0.001$). Niche overlap was 0.53.

Our results support models predicting resource partitioning between alternative morphs (11). In such models, behavioral, physiological and morphological differences between morphs make them more successful in using specific resources. Paedomorphs are particularly expected in deep waters because of their larval traits, notably a gilled mode of respiration. The relative highest abundance of paedomorphic palmate newts in the deepest parts of the two studied ponds confirms this expectation. This was particularly the case in Canourgue-Groupilliers, with a niche overlap of 53% (76% at Le Coulet). Other studies of a related species, the Alpine newt, gave varied results. Although strong resource partitioning was observed in deep lakes (2), fewer differences were found in an Italian farmer pond (7). This can be explained by habitat complexity as ponds are not so diversified (cf. microhabitats) than lakes. In the present case study, habitat partitioning is not so strong as in the French Alpine lake (2), but higher than in the Italian pond (7). Both studied Larzac ponds are deep: around 2 m depth in spring, compared to only 0.7 m depth for the Italian pond. They thus present a vertical component similar to that of the deepest lakes (2, 6). Habitat segregation between morphs was found in the two sexes, but particularly in males. Not all Larzac ponds inhabited by facultatively dimorphic palmate newts are deep. In some ponds, this is caused by high evaporation or infiltration processes. In other ponds, this is caused only by the shape of the ponds, built to re-

tain less water. In these shallower habitats (less than 1 m maximum depth), there is not as much space for habitat partitioning. Explaining the persistence of dimorphism thus requires the understanding of other causes, such as life-history traits (notably age structure). Future studies should focus on these points, and particularly on behavioral changes with habitat modification caused by natural drying and human influence.

References and Notes

- Griffiths R.A. 1996. Newts and Salamanders of Europe. T. & A.D. Poyser Ltd., London.
- 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.
- Semlitsch R.D. 1987. Paedomorphosis in *Ambystoma talpoideum*: effects of density, food, and pond drying. *Ecology* 68, 994–1002.
- Denoël M. 2003. How do paedomorphic newts cope with lake drying? *Ecography* 26, 405–410.
- 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.
- Denoël M., Schabetsberger R. 2003. Resource use in two heterochronic populations of Greek Alpine newts, *Triturus alpestris veluchiensis* (Wolterstorff, 1935). *Acta Oecol.* 24, 55–64.
- Denoël M., Andreone F. 2003. Trophic habits and microhabitat use in gilled immature, paedomorphic and metamorphic Alpine newts (*Triturus alpestris apuanus*) at a pond in central Italy. *Belg. J. Zool.* 133, 95–102.
- Gabrion J., Sentein P., Gabrion C. 1977. Les populations néoténiques de *Triturus helveticus* Raz. des Causses et du Bas-Languedoc. I. Répartition et caractéristiques. *Terre et Vie* 31, 489–506.
- Denoël M., Duguet R., Dzukic G., Kalezić M., Mazzotti S. 2001. Biogeography and ecology of paedomorphosis in *Triturus alpestris* (Amphibia, Caudata). *J. Biogeogr.* 28, 1271–1280.
- Schoener T.W. 1974. Resource partitioning in ecological communities. *Science* 185, 27–39.
- Skulason S., Smith T.B. 1995. Resource polymorphisms in vertebrates. *Trends Ecol. Evol.* 10, 366–370. 12.

Thanks to J.M. Burisi and P. Perrier for allowing access to their ponds, M. Albrecht and A. Spina for their constructive comments on the manuscript, F. Hourlay for helping with the field work, and Hérault Prefecture for giving authorization to study newts. This research benefited from FNRS grant number 1.5.011.03 and 1.5.120.04 (Crédit aux chercheurs).

© Royal Swedish Academy of Sciences 2005

Mathieu Denoël
 FNRS Postdoctoral Researcher
 Laboratory of Fish and Amphibian Ethology
 Behavioural Biology Unit
 Department of Environmental Sciences
 University of Liège
 22 Quai van Beneden
 4020 Liège,
 Belgium
 Mathieu.Denoel [at] ulg.ac.be