

How do paedomorphic newts cope with lake drying?

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Paedomorphosis, in which adult individuals retain larval traits, is widespread in newts and salamanders. Most evolutionary models predict the maintenance of this life-history trait in favourable aquatic habitats surrounded by hostile terrestrial environments. Nevertheless, numerous ponds inhabited by paedomorphic individuals are unpredictable and temporary. In an experimental framework, I showed that paedomorphic newts were able to metamorphose and thus survive in the absence of water. However, the mere decrease of water level or the life space do not seem to induce metamorphosis in paedomorphs. On the contrary, drying up induces almost all individuals to move on land and after that to colonize other aquatic sites located nearby. Such terrestrial migrations allow survival in drying conditions without metamorphosis as long as the distances of terrestrial migration are short. These results are consistent with the presence of paedomorphs in drying ponds and are in favor of classic optimality models predicting metamorphosis in unfavorable environments.

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Paedomorphosis is a heterochronic process in which subadult traits are retained in the adults (Gould 1977). In newts and salamanders, this means the retention of gills and gill slits. In some species, mature larvae never transform (obligate paedomorphosis); in others, both developmental pathways coexist (facultative paedomorphosis) (Semlitsch and Wilbur 1989, Whiteman 1994). These processes have profound ecological and evolutionary implications (McKinney and McNamara 1991) and result in large variations in morphology and habitat use (aquatic vs terrestrial) (Whiteman et al. 1996).

Facultative paedomorphosis is a polyphenism that allows newt to cope with environmental change. Experimental results have shown that permanent water, low density and high food level all favour a paedomorphic ontogenetic pathway, whereas drying, high density and fasting induce metamorphosis (Harris 1987, Semlitsch 1987, Denoël and Poncin 2001). Such phenotypic plasticity is adaptive in allowing high growth rates in

favourable aquatic environments and survival in hostile temporary waters. Most of the evolutionary models predict paedomorphosis when aquatic life is more profitable than the terrestrial one (Wilbur and Collins 1973, Werner 1986, Whiteman 1994).

Paedomorphic populations have been found in small water bodies and even in temporary ponds, some of them drying each year, others only in some years (Healy 1974, Dzukic and Kalezic 1984, Breuil 1992, Denoël 1997, Denoël et al. 2001a). In such places, paedomorphosis was shown to be adaptive in allowing earlier reproduction (Denoël and Joly 2000). Amphibian larvae can accelerate metamorphosis in drying ponds (Newman 1989, Denver et al. 1998, Laurila and Kujasalo 1999) and thus avoid death due to desiccation. Obligate paedomorphs, such as sirenids, but also several species of fishes, can also cope with lake drying by burrowing into the substrate (Johnels and Svensson 1954, Gelbach et al. 1973) and protecting themselves from water loss by secreting a cocoon (Ruibal and

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Hillmans 1981, Etheridge 1990). Some fish species can perform terrestrial migrations to reach another pond (Inger 1952, Johnels 1957), but it is still unknown if branchiate amphibians can cope with lake drying in this way.

The objective of this study was to test the developmental and behavioural effect of pond drying on paedomorphic Alpine newts *Triturus alpestris* (Laurenti 1768) (Amphibia, Caudata, Salamandridae), in the framework of evolutionary models on paedomorphosis (Wilbur and Collins 1973, Whiteman 1994). Particularly, I explored whether paedomorphs are capable of metamorphosis and thus of survival and changing habitat during desiccation, and whether they can migrate on land without metamorphosis in response to drying.

Methods

Origin and maintenance of newts

Alpine newts *Triturus alpestris* were caught with a landing net at La Cabane Lake in the French Alps (44°24'N/06°24'E; 1950 m elevation). In this lake, water level varies drastically during the year, with a tidal range > 5 m. In summer, drying up splits the lake into two parts. The deepest one retains water but the shallowest totally dries up. Newts were kept in refrigerated boxes (5–10°C; 30 × 20 × 12 cm) to transport them to the laboratory. Temperature was 15°C and photoperiod 14 L/10 D. *Chironomus* larvae were provided daily as food (70 mg per newt). This food level constitutes a non-limiting factor (Denoël and Joly 2001b, Denoël and Poncin 2001). No food was provided in experiment 3 to simulate the situation occurring after completion of a drying up. These values are within the range met by the newts in their lake. The substrate of the laboratory aquariums was composed of gravel.

An individual was classified as a metamorph when gill slits were closed, and as a paedomorph when gill slits were open. Both paedomorphs and metamorphs are adults (Denoël et al. 2001b).

Experiment 1: effect of progressive drying and space without possibility of migration

During drying in natural populations, the water level decreases, but also the newt density increases as a result of the decrease in aquatic space. This first experiment was designed to evaluate whether paedomorphs can accelerate metamorphosis in response to a decline in the water level or to a reduction of their aquatic habitat. Eighty paedomorphic Alpine newts were caught at La Cabane Lake. They were randomly distributed into eight aquaria (10 individuals per aquarium). Six aquaria were used to test the effect of space (“density”)

and two aquaria to test the effect of water level decrease (“drying”). Reducing space rather than increasing the number of individuals allows identical sampling sizes for statistical comparisons and limits the sampling pressure in natural populations according to ethical considerations (Denoël et al. 2001a). Three different water volumes were used, with two replicates for each (i.e. 42, 84, and 168 l for a bottom surface of 12, 24 and 48 dm² respectively), which mean densities of 0.24 (HDS: high density – stable), 0.12 (MDS: mid-density – stable) and 0.06 ind. l⁻¹ (LDS: low density – stable). Water level was kept constant at 35 cm in these six aquaria. Pond drying was simulated in two other aquaria (168 l at maximum water level for a bottom surface of 48 dm²). This was done by removing water (one cm) every four days to a depth of eight cm. That means densities vary from 0.06 to 0.26 ind. l⁻¹ (LDU: low density – unstable). Because removing water could constitute a disturbing element, this act was simulated in the other aquaria but without eliminating water. To counter-balance the density effect of mortality, dead newts were replaced by living ones. These individuals were marked (toe-clipping) to avoid confusion with the newts that are used in the experiment.

Experiment 2: effect of progressive drying and density with possibility of migration

In this experiment I examined whether paedomorphic newts are able to leave the water and migrate onto land in response to decreasing water level and reduced space. One hundred and twenty paedomorphic Alpine newts were caught with a landing net at La Cabane Lake. I used two 250 × 60 cm aquaria that were divided into two equal compartments with a 38 cm high vertical barrier in-between (Fig. 1). A gravel slope built in the right part of the aquarium and a platform gave access to the left part. Movement from the left part to the right part was impossible. Ten paedomorphic individuals were put in the right part of each aquarium. I checked daily the position of each newt (left or right part) over 21 d. I conducted three treatments. In the first one (control: FSS = full space – stable), the water level was kept stable (38 cm) and all the right part of the aquarium was left accessible to the newts

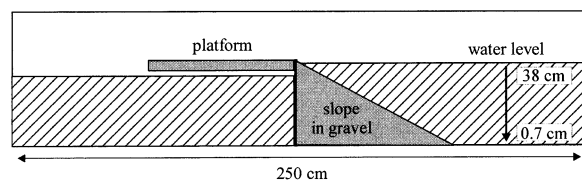


Fig. 1. Experimental aquarium in which a progressive drying was simulated (right side) and in which a migration was possible to the left part by means of a slope and a platform.

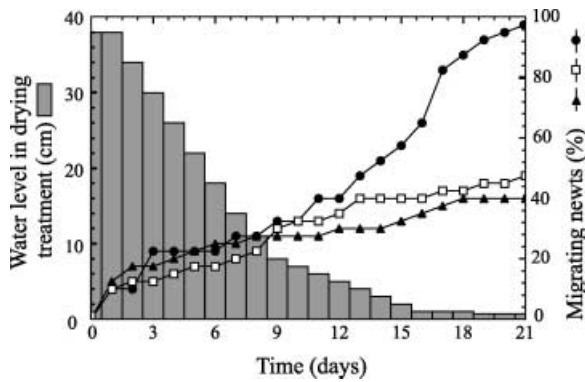


Fig. 2. Effect of drying and density on the terrestrial migration date of pedomorphs. Full circles: full space – decline in water level; open boxes: reduced space – stable water level; full triangles: full space – stable water level. Each treatment was replicated four times (10 newts in each replicate). For statistics, see Table 2.

(i.e. 125 × 60 cm; 200 l). In the second one (FSU = full space – unstable), the water level was decreased from 38 to 0.7 cm (Fig. 2) and all the right part of the aquarium was also left accessible to the newts. In the third one (RSS = reduced space – stable), the water level was kept stable (38 cm), but newts were only allowed to occupy a portion of the right part of the aquarium (140 l), as a result of the placement of walls. These three treatments were each replicated four times.

Experiment 3: effect of water and food deprivation

This experiment tested whether pedomorphic newts are able to metamorphose and thus to change habitat in response to water and food deprivation, two conditions occurring just after lake drying. Twenty-two pedomorphic Alpine newts were caught with a landing net at La Cabane Lake. They were placed during one month in two 250 × 30 cm aquaria filled with water (35 cm deep), with 11 individuals in each. Water was then removed but gravel was kept wet. Three slates were placed in each aquarium to constitute a shelter for the newts. Newts were checked every two days over 40 d.

Statistical procedures

The aim of the analysis was to compare the dates of migration and metamorphosis of pedomorphs between treatments. It is inappropriate to use standard non-parametric tests because some individuals did not migrate or did not metamorphose by the end of the experiments. These data are then called censored because it is only known that the event of interest (migration, metamorphosis) is at least later than a given point

of time. The way to analyse these data is to use a survival analysis, which take into account the distribution of life times, i.e. the times from an initiating event (e.g. start of the experiment) to some terminal event (e.g. metamorphosis) (Andersen and Keiding 1998). I tested the null hypothesis of two equal survival functions in treatments with a generalized Wilcoxon-Gehan test. This test puts more weight on the observations made at the beginning and because of that its use is more powerful in detecting the effects of short-term terminal events. It is derived from the classical Wilcoxon rank-sum test and is equivalent to it in the absence of censoring (Chap 1997, Anon. 2000).

Results

Experiment 1: effect of long-term drying and density without possibility of migration

Thirty pedomorphic newts metamorphosed, 46 remained pedomorphs and four died. Only seven individuals metamorphosed during the first half of the experiment (i.e. 60 d). Cases of metamorphosis occurred in all treatments: low density – stable (n = 6), mid-density – stable (n = 9), high density – stable (n = 9), low density – unstable (n = 6). Newts that did not metamorphose showed slight signs of metamorphosis (gill regressions) by the end of the experiment. However, their gill slits were always open. No difference was found between replicates within treatments. Neither density nor water level stability affected time of metamorphosis (Wilcoxon test, $p > 0.05$, Table 1).

Experiment 2: effect of progressive drying and density with possibility of migration

During the three weeks of experiments, 73 pedomorphic Alpine newts left water and migrated on land while 47 remained in the right parts of the aquaria (Figs 1 and 2). Dates of migration did not vary within treatments, except in reduced space experiments

Table 1. Effect of density and drying up on the dates of metamorphosis (Wilcoxon-Gehan test). Treatments: LDS (low density stable), MDS (mid density stable), HDS (high density stable), LDU (low density unstable). Two replicates for each treatment (n = 10 in each).

Comparison	Wilcoxon test	p
LDS × MDS	1.850	0.06
LDS × HDS	1.642	0.10
MDS × HDS	0.214	0.83
LDS × LDU	0.506	0.61
replicate LDS	0	1
replicate MDS	1.148	0.25
replicate HDS	-1.757	0.78
replicate LDU	-0.887	0.38

Table 2. Effect of density and drying up on the dates of terrestrial migration (Wilcoxon-Gehan test). Treatments: FSS (full space – stable water level), FSU (full space – unstable water level), and RSS (reduced space – stable water level). Four replicates for each treatment (n = 10 in each).

Comparison	Wilcoxon test	p
FSS × FSU	3.281	0.001
FSS × RSS	0.184	0.85
FSU × RSS	–3.016	0.003
replicate FSS	1.391	0.70
replicate FSU	2.392	0.50
replicate RSS	10.950	0.01

(Wilcoxon test, $p < 0.01$, Table 2). Although newts showed terrestrial migrations in all treatments (stable water level in full and reduced space, decreasing water level in full space), they did so mainly when water level was decreased. The difference is significant (Wilcoxon test, $p < 0.01$, Table 2, Fig. 2). Ninety-five percent of newts left the water under such conditions (4 replicates, 10 newts in each), whereas $< 50\%$ did so in the other treatments (2×4 replicates, 10 newts in each). The paedomorphs that migrated did not metamorphose by the end of the experiment. All individuals survived the experiment.

Experiment 3: effect of water and food deprivation

Twenty paedomorphic individuals metamorphosed during the total drying experiment. Two died without metamorphosing. The two replicates did not significantly differ in the days of metamorphosis (Wilcoxon test, $p = 0.36$). Metamorphosis took place at different dates between day 8 and 38 after the start of the dry conditions, but most of the events occurred between day 12 and 24 (Fig. 3).

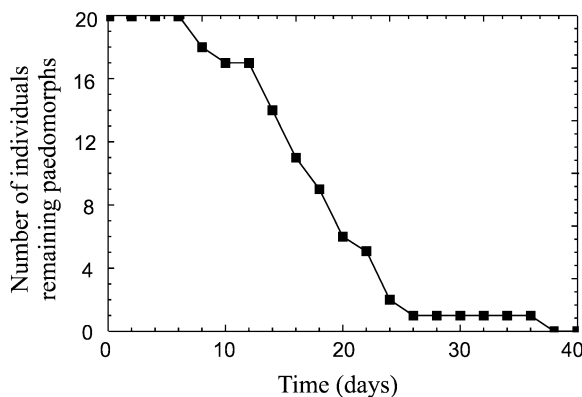


Fig. 3. Effect of total drying on metamorphosis date of paedomorphs (n = 20 ind.).

Discussion

These results show that more than one solution is given to the newts in case of habitat deterioration such as drying up. Additionally to the known fact that paedomorphs are able to metamorphose (Breuil 1992, Denoël and Poncin 2001), I present here the evidence that paedomorphic individuals can move on land without undergoing a metamorphosis, keeping then their larval structure when they reach water again. Paedomorphosis is thus a polyphenism that allows individuals to cope with environmental changes (West-Eberhard 1989). However, not all the drying experiments produced metamorphs.

On the basis of Wilbur and Collins's model (1973), called the "paedomorph advantage hypothesis" by Whiteman (1994), larvae growing in a favourable permanent aquatic habitat should maximize their fitness in becoming paedomorphs, thus avoiding the cost of metamorphosis and of colonizing a hostile terrestrial environment. Metamorphosis of paedomorphic Alpine newts in absence of water supports this cost-benefit model for adult individuals. Through metamorphosis, paedomorphs escape an unfavourable aquatic environment (e.g. for survival) and then can survive and potentially colonize other ponds. Such a response allows individuals to cope better with environmental change, a trait that is beneficial in these animals that often breed in unstable aquatic habitats (Healy 1974, Breuil 1992, Denoël 1997, Denoël and Joly 2000, Denoël et al. 2001b). Because the absence of prey can induce metamorphosis in paedomorphs (Denoël and Poncin 2001), it may partially explain its occurrence in the experience during which all the water was removed. However, all individuals metamorphosed in this experiment vs only 50% in food deprivation experiment (Denoël and Poncin 2001).

The mere decrease of water level causes ambystomatid larvae to opt for metamorphosis instead of paedomorphosis (Semlitsch 1987, Semlitsch and Wilbur 1989). High density also favours a metamorphic life-history pathway (Harris 1987, Semlitsch 1987). When the quality of the aquatic habitat decreases (e.g. risk of desiccation), larvae undergo metamorphosis and avoid competition or mortality. However, in my experiments with paedomorphic Alpine newts, I did not find any effect of density and stability of water level. Some paedomorphs metamorphosed in all treatments. High density and drying treatments produced as many metamorphs as low density and permanent water. From a general point of view, these responses do not seem adaptive. However, in lake La Cabane, the maintenance of dimorphism confers a better use of resources, each morph occupying specific micro-habitats and feeding on particular prey (Denoël and Joly 2001a, b). Because of drying up, this lake splits into two parts. Each year, the shallow basin dries out while the deepest

one retains water all the year. If paedomorphs metamorphose each year when the lake dries out, they would lose resources (plankton) for which they are better forager than metamorphs (Denoël 2001, Denoël and Joly 2001a, b). By remaining paedomorphs in the case of lake drying and by being capable of terrestrial migration to the permanent basin (see beneath), the individuals retain then a favourable trophic structure which confers them higher performance (Denoël 2001).

When the possibility of terrestrial migration was offered, paedomorphs migrated on land to reach a part of the aquarium filled with water. Most of the individuals migrated in such a way, but they mainly did so in experiments during which water level was decreased. Alpine newts can thus detect cues of the drying up. By being able to cross terrestrial habitats, they retain their aquatic phenotype when they arrive in other aquatic sites. Direct observations in the field showed that paedomorphs are able to migrate on land to survive to pond drying. Such migrations occur up to at least twenty meters. Capture-mark-recapture experiments also confirm the absence of metamorphosis of almost all paedomorphs during the drying of the shallow basin of La Cabane Lake (Denoël unpubl.). However, the experiments, during which all the water was removed, showed that to be effective (i.e. without metamorphosis) paedomorph migration has to be short as a long stay on land induces metamorphosis. Such migrations, even on short distances had never before been reported for paedomorphic newts and salamanders although such a process is known in cat-fishes (Inger 1952, Johnels 1957).

Some fish and amphibian species are known to burrow into the sediment (e.g. *Siren intermedia*: Gelbach et al. 1973; *Protopterus annectens*: Johnels and Svensson 1954) or to secrete a cocoon to protect themselves from desiccation (e.g. *Lepidobatrachus llanensis*: McClanahan et al. 1976; *Pterohyla fodiens*: Ruibal and Hillmans 1981; *Siren lacertina* Etheridge 1990). In the experimental design presented here, the substrate of the aquariums was composed of hard substrate which does not allow burrowing. However, paedomorphic newts reared on soft substrate (clay) were never seen burrowing into the wet sediment after water was removed (unpubl.). No trace of cocoon was observed around the newts in any of the experiments.

Not all the individuals reacted in the same way when confronted with an identical environment. Migrations occurred at different dates: from the first day to the 21st day of the experiment. In drying and density experiments without possibilities of migration, some newts metamorphosed while the others remained paedomorphs. Differences in reacting to environmental cues may result from age or genetic differences between individuals. It could also be interpreted as a kind of diversified bet-hedging or coin-flipping strategy (Kaplan and Cooper 1984, Menu and Debouzie 1993,

Hopper 1999). If the aquatic habitat offers a large spectrum of resources and good growing conditions, it could be disadvantageous to metamorphose and leave water for land, particularly when the terrestrial environment is unfavourable (paedomorph advantage hypothesis: Wilbur and Collins 1973, Whiteman 1994). However, if an individual waits too long before metamorphosing or migrating, it risks death because of desiccation and/or predation. In such unpredictable habitats, detection of cues is certainly adaptive in allowing survival (Wilbur 1990, Newman 1992, Denver et al. 1998). However, a valuable strategy may then consist of spreading the risks instead of responding directly to the first cues of lake drying. Such a strategy would result in metamorphosis or migration at different dates close to the optimum time.

Depending on the structure of the aquatic and terrestrial habitats, paedomorphic newts can react in different ways. They are able, both to metamorphose and thus to survive desiccation, but also to migrate on land when other aquatic sites are reachable. Further studies on complexes of temporary-permanent ponds containing both metamorphic and paedomorphic individuals would certainly be promising in the understanding of the maintenance of facultative paedomorphosis in the framework of metapopulation theory.

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