How do paedomorphic newts cope with lake drying?

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Abstract

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.

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, Whitman 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) (Whitman 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, Whitman 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 sirens, 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 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, Whitman 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 aquaria 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 24 cm. That means densities vary from 0.06 to 0.26 ind. l⁻¹ (LDS: low density – unstable). Because removing water could constitute a disturbing element, this act was simulated in the other aquaria but without eliminating water. To counterbalance 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 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 (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 left also 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 paedomorphic 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 paedomorphic 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. News 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 paedomorphs 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.

**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).

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Wilcoxon test</th>
<th>P</th>
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<tbody>
<tr>
<td>LDS×MDS</td>
<td>1.850</td>
<td>0.06</td>
</tr>
<tr>
<td>LDS×HDS</td>
<td>1.642</td>
<td>0.10</td>
</tr>
<tr>
<td>MDS×HDS</td>
<td>0.214</td>
<td>0.83</td>
</tr>
<tr>
<td>LDS×LDU</td>
<td>0.506</td>
<td>0.61</td>
</tr>
<tr>
<td>replicate LDS</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>replicate MDS</td>
<td>1.148</td>
<td>0.25</td>
</tr>
<tr>
<td>replicate HDS</td>
<td>−1.757</td>
<td>0.78</td>
</tr>
<tr>
<td>replicate LDU</td>
<td>−0.887</td>
<td>0.38</td>
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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 paedomorphic newts metamorphosed, 46 remained paedomorphs 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 paedomorphic 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 (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 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 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. 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).

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).

<table>
<thead>
<tr>
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<th>P</th>
</tr>
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<tbody>
<tr>
<td>FSS×FSU</td>
<td>3.281</td>
<td>0.001</td>
</tr>
<tr>
<td>FSS×RSS</td>
<td>0.184</td>
<td>0.85</td>
</tr>
<tr>
<td>FSU×RSS</td>
<td>-3.016</td>
<td>0.003</td>
</tr>
<tr>
<td>replicate FSS</td>
<td>1.391</td>
<td>0.70</td>
</tr>
<tr>
<td>replicate FSU</td>
<td>2.392</td>
<td>0.50</td>
</tr>
<tr>
<td>replicate RSS</td>
<td>10.950</td>
<td>0.01</td>
</tr>
</tbody>
</table>

Fig. 2. Effect of drying and density on the terrestrial migration date of paedomorphs. 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

**Experiment 3: effect of water and food deprivation**

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.

Discussion

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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 amby-
somatotid larvae to opt for metamorphosis instead of
paedomorphosis (Semlitsch 1987, Semlitsch and
Wilbur 1989). High density also favours a metamor-
phic life-history pathway (Harris 1987, Semlitsch
1987). When the quality of the aquatic habitat de-
creases (e.g. risk of desiccation), larvae undergo
metamorphosis and avoid competition or morta-
ality. However, in my experiments with paedomor-
phic Alpine newts, I did not find any effect of den-
sity and stability of water level. Some paedomor-
phs 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 fee-
ding 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 deep-
est 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 paedomor-
phs 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 perfor-
mance (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 observation 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, du-
rine which all this water was removed, showed that
to be effective (i.e. without metamorphosis) paedo-
morph 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: John-
nels and Svensson 1954) or to secrete a cocoon to
protect themselves from desiccation (e.g. Lepido-
batrachus llanensis: McClanahan et al. 1976; Pter-
nothyla fodiens: Ruibal and Hillmans 1981; Siren la-
certina:Etheridge 1990). In the experimental design
presented here, the substrate of the aquarium 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 migra-
tion, some newts metamorphosed while the others
remained paedomorphs. Differences in reacting to
environmental cues may result from age or gene-
tic 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 disadvan-
tageous to metamorphose and leave water for
particular environments, detection of cues is certainly adaptive in
allowing survival (Wilbur 1990, Newman 1992,
Denver et al. 1998). However, if an individual waits too long before meta-
morphosing 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 meta-
morphose and to survive desiccation, but also to
migrate on land when other aquatic sites are rea-
achable. Further studies on complexes of tempo-
rary-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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