Neoteny and progenesis as two heterochronic processes involved in paedomorphosis in *Triturus alpestris* (Amphibia: Caudata)

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Abstract

Current theories on the evolution of paedomorphosis suppose that several ontogenetic pathways have appeared according to different selective pressures. The aim of of this study was to find out whether two distinct processes can lead to paedomorphosis in the Alpine newt, *Triturus alpestris*. In this respect, we compared age structures of paedomorphic and metamorphic individuals in two newt populations where the two forms lived syntopically. Whereas paedomorphosis resulted in a slower rate of somatic development in one population, it resulted in an acceleration of sexual maturation in the other population. These processes correspond to neoteny and progenesis, respectively. These results suggest that phenotypic plasticity can result from contrasted ontogenetic pathways between two populations of the same species. They give support to models that consider gonadic development as the target of selection under different environmental pressures.

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1. Introduction

As small changes in genes controlling ontogeny can induce large phenotypic variation, developmental heterochronies are suspected to play an important role in both micro- and macroevolutionary processes (Gould 1977; McKinney & McNamara 1991; McNamara 1997). Such developmental heterochronies have been evidenced in many animal groups such as mammals (Fiorello & German 1997), birds (Livezey 1992), amphibians (Wilbur & Collins 1973; Emerson 1986), fishes (Meyer 1987) and invertebrates (Harvell 1994). Heterochrony consists of shifts in relative timing or development rate of a given biological trait (McKinney & McNamara 1991). Underdevelopment or overdevelopment of a trait relatively to the ontogenetic course of this trait in the ancestor correspond to paedomorphosis or peramorphosis, respectively (Alberch et al. 1979). Heterochrony may originate in phenotypic plasticity that results as a response to a varying environment (Scheiner 1993, Schlichting & Pigliucci 1995).

In newts and salamanders, paedomorphosis is defined as the retention of larval traits such as gill slits and external gills in reproducing adults (Gould 1977; Semlitsch & Wilbur 1989). Among the salamander families, four are considered to be obligate paedomorphs because they have lost the ability to undergo complete metamorphosis. In the other families, paedomorphosis results from phenotypic plasticity as it is expressed by only a proportion of the individuals in a population (facultative paedomorphosis within the genera *Ambystoma* and *Triturus*) (Duellman & Trueb 1985; Whiteman 1994). Moreover, facultative paedomorphosis has been proved reversible, as paedomorphic individuals can experience metamorphosis (Semlitsch 1987). Several authors consider that paedomorphosis is an alternative ontogenetic pathway that should increase fitness in variable habitats (Whiteman 1994, Ryan & Semlitsch 1998). Although the evolution of plasticity in amphibians has been documented (Semlitsch et al. 1990), the determinants of each alternative remain poorly understood. Whiteman (1994) has proposed evolutionary scenarios that link larval growth to the probability of becoming paedomorph. While his "best of a bad lot" hypothesis could explain patterns observed in some high altitudinal lakes (low growth and permanent water), his "paedomorph advantage" hypothesis found an experimental support in studies demonstrating that paedomorphosis could be a response to favourable aquatic conditions such as low density (Harris 1987; Semlitsch 1987), permanent water (Semlitsch 1987), and absence of fish (Jackson & Semlitsch 1993). Under such favourable conditions, paedomorphosis was proven adaptive in allowing a better rate of prey capture (Reilly & Lauder 1988; Whiteman et al. 1996), earlier mating (Krenz & Sever 1995), and, in males, a shorter time interval between breeding events (Whiteman 1997). Moreo-

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ver, paedomorphosis was shown to reduce competition through resource partitioning (Fasola 1993; M. Denoël & P. Joly, unpublished data). A genetic underpinning of paedomorphosis has also been demonstrated (Semlitsch & Wilbur 1989; Harris et al. 1990; Semlitsch et al. 1990; Voss 1995; Shaffer and Voss 1996; Voss and Shaffer 1997).

Gould (1977) recognized neoteny and progenesis as two processes that produce paedomorphic phenotypes (deceleration and hypomorphosis, respectively, in Reilly et al. 1997). Both processes imply a retardation of somatic development. They differ in that first reproduction occurring in neotenic individuals at the same age as in metamorphosed individuals, whereas it occurs at an earlier age in progenetic individuals. The process by which sexual development is decoupled from somatic development is of particular interest (Ryan & Semlitsch 1998) because sexual maturation has been shown to respond to selective pressures (Roff 1992; Stearns 1992). Neoteny and progenesis differ in their life history and ecological implications. In lowering age at first reproduction, progenesis is expected to shorten generation time and imply a smaller body size. In contrast, neoteny is not expected to deeply modify individual life history but to promote niche partitioning in allowing paedomorphic individuals to use deeper waters than metamorphosed individuals (M. Denoël & P. Joly, unpublished data).

In newts and salamanders, paedomorphosis is usually considered to result in neoteny (Gould 1977; Gilbert 1994; Raff 1996; Ridley 1996; Smith & Skulason 1996). This hypothesis has been recently supported by skeletochronological data in two natural populations of newts (Kalezic et al. 1996). However, several studies have also brought evidence for progenesis from body size analysis (Healy 1974; Bruce 1979; McNamara 1997). In an experimental framework, Harris (1987) could conclude neither on progenesis nor on neoteny as the metamorphs and paedomorphs who lived in syntopy under water reached maturity at the same age, whereas the metamorphs that lived on land matured later. In a laboratory study focusing on age at first reproduction in *Ambystoma*, Ryan & Semlitsch (1998) demonstrated earlier maturation in paedomorphs than in metamorphs, but without growth variation.

These confusing results can rely on variation of paedomorphosis determinism among populations experiencing contrasted ecological conditions. In this context, our aim was to compare age structures of paedomorphic (=derived state) and metamorphic (=ancestral state) individuals living syntopically in two natural populations of the Alpine newt *Triturus alpestris*. The ecological conditions of these populations greatly differed as one occupied a lowland temporary water while the other one occupied a deep alpine lake. This study took advantage of skeletochronology, which makes it possible to compare age structures at the same dates in the same site, for obtaining secure estimation of individual ages.

2. Materials and Methods

We studied two populations of the Alpine newt *T. alpestris*. Population A was investigated at an Alpine lake (elevation 1950m above sea level) located in the Southern Alps (lac de la Cabane, Alpes-de-Haute-Provence, France, UTM: 32TKQ91). After thawing, maximum depth usually reaches 7 m, area 0.75 ha and volume 25000m³. During summer, depth usually decreases until it is 1.5 m, area 0.15 ha, and volume 1500m³. The lake is surrounded by conife-

rous trees and Alpine lawn. Population B occupied a pond located in the Appenines (Parana, Tuscany, Italy, UTM: 32TNQ60, 600m elevation). The maximum depth of this pond is 0.7 m for a 200m² area and a 100m³ volume. This pond is surrounded by pastures and deciduous forests.

The newts were sampled by dip-netting. After being anaesthesized by phenoxyethanol, newts were measured and weighted (Joly & Miaud 1989b). Sexual maturity was established on the basis of a developed cloaca, and sexes on the presence of secundary sexual characteritics (e.g. shape of the cloaca). An individual was called paedomorphic if gill slits were open.

Population sizes were estimated on the basis of the Petersen index using capture-marking-recapture data. A 95% confidence limit was used: it is shown between brackets following the estimate of population size (Greenwood 1999). Marks were made by tattooing (Joly & Miaud 1989a). In population A, sampling was performed between 9 and 12 October 1997 and in population B between 21 and 23 March 1997. We consider that there were no emigration, immigration or mortality during the experiment. Other samples were taken to determine the population structure in June, July, August and October 1997, May and October 1998, and May and October 1999 (population A) and in April 1997 and March 1998 (population B).

The longest digit from the hindfoot of the newts was cut and individually stored in 75% ethanol. Age was estimated using these bone samples. The procedure followed previous descriptions (e.g. Miaud et al. 1993; Wake & Castanet 1995): after removing muscle and skin, bones were decalcified during 45 min in 3% nitric acid and then washed in tap water over night. Cross sections (16 μm) were performed in the diaphyseal region using a freezing microtome. They were stained with Ehrlich's haematoxylin by immersion for 15 min, washed in distilled water for a few minutes and mounted. This method made age estimation possible in 116 adult newts in population A (30 male paedomorphs, 32 female paedomorphs, 27 male metamorphs, 27 female metamorphs) and in 129 adult newts in population B (28 male paedomorphs, 32 female paedomorphs, 37 male metamorphs, 32 female metamorphs).

As age structures did not fit normal distributions (Kolmogornov-Smirnov test), we used Mann-Whitney *U*-test for all statistical comparisons. Distributions of body sizes were compared with Student's *t*-statistic (maximum error risk = 0.05) (Siegel & Castellan 1988; Statsoft 1996).

3. Results

(a) Population A

As 144 newts were marked at the first capture session and 105 caught at the second one, from which 14 were marked, population size was estimated to reach 1014 (720 - 2167) adults, which gives a density of 0.7 (0.5 - 1.5) newts per cubic metre in October. Paedomorphs outnumbered metamorphs in each sample. They acounted for 77% of the adult population in June 1997 ($n = 210$), 82% in July 1997 ($n = 175$), 80% in August 1997 ($n = 293$), 85% in October 1997 ($n = 258$), 80% in May 1998 ($n = 332$), 83% in October 1998 ($n = 458$), 73% in May 1999 ($n = 374$) and 78% in October 1999 ($n = 695$).

In males, age structures did not differ significantly between paedomorphs ($n = 30$) and metamorphs ($n = 27$) ($U = 337$, $p = 0.28$). But in females they dif-
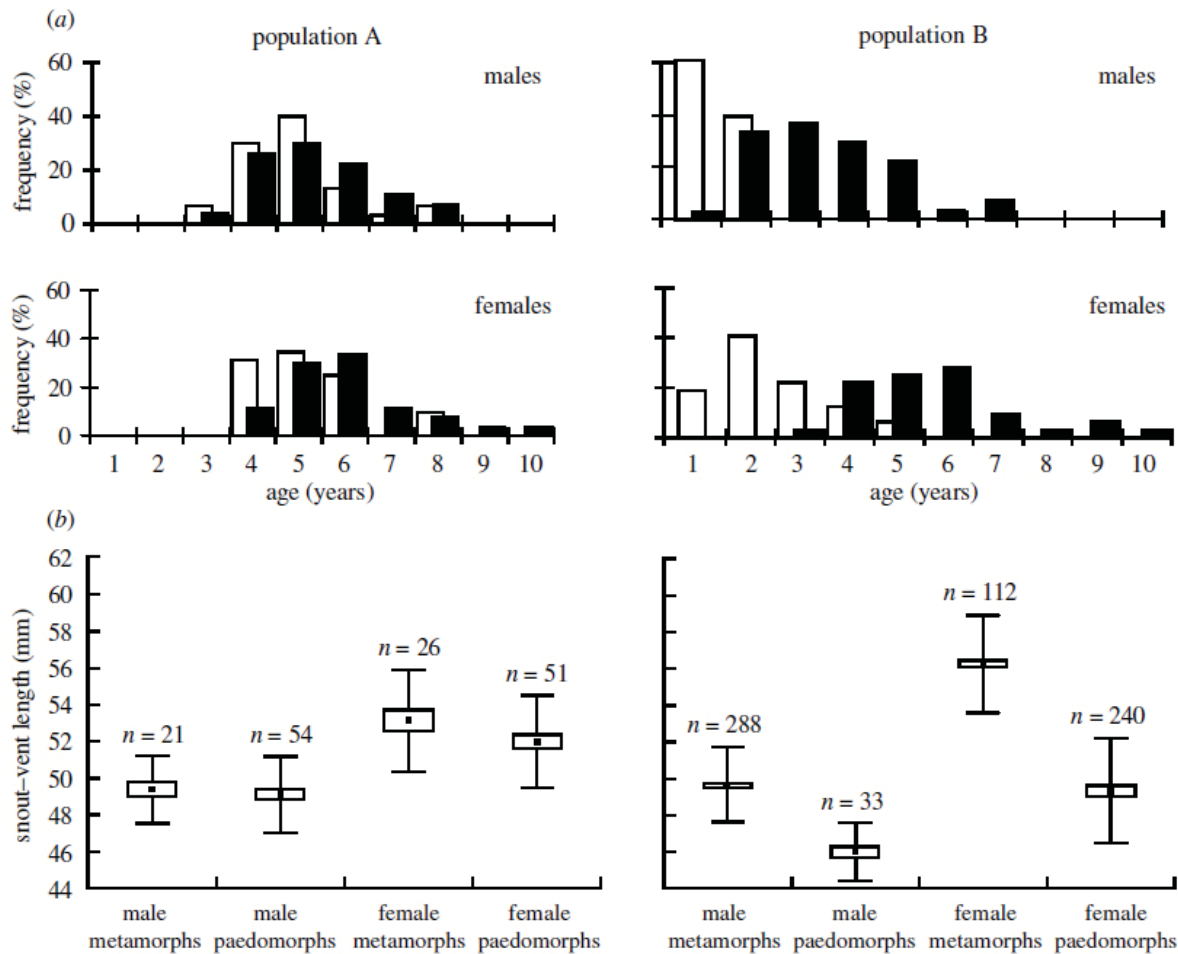
Figure 1. Age and size structures of paedomorphs and metamorphs of sites A and B. (*a*) Age of the two morphs significantly differs in females (U = 288, p = 0.03) in site A, and in both sexes in site B (males: $U = 69$, $p < 0.0001$; females: $U = 45.5$, $p < 0.0001$). (*b*) Size (snout-vent length) of the two morphs significantly differs in site B (males: $t_{319} = -9.91$, p < 0.0001; females: $t_{350} = -22.25$, $p < 0.0001$). Whiskers, s.d.; box, s.e.; point, mean.

fered slightly but significantly with paedomorphic females maturing earlier than metamorphic ones ($U = 288$, $p = 0.03$, $n = 32$ and 27 respectively). Age at first reproduction was three to four years in males and four to five years in females. Longevity of males was eight years in both morphs whereas in females it was eight years in paedomorphs, and ten years in metamorphs (figure 1*a*). The median age was five years for each newt category, except for metamorphosed females in which it was six years.

Mean body sizes (snout-vent length) were similar in both paedomorphic and metamorphic males ($t_{73} = -0.52$, $p = 0.6$) and females ($t_{75} = -1.78$, $p = 0.08$; figure 1*b*).

(b) Population B

We marked 368 newts at the first capture session and caught 624 at the second one, of which 99 were marked. Population was estimated at 2305 (2000 - 2760) adults, which gives a density of 23 (20 - 28) newts per cubic metre. Paedomorphs were outnumbered by metamorphs in each sample: they accounted for 22% in April 1997 ($n = 674$) and 1% in March 1998 ($n = 891$).

Age structures largely differed widely between paedomorphs and metamorphs (males: $U = 69$, $p < 0.0001$; females: $U = 45,5$, $p < 0.0001$). The me-

dians were one and three years for paedomorphic and metamorphic males, respectively, and two and five years for females. Most paedomorphic males reached maturity when one year old while most metamorphic males reached maturity later when two or three. In females this difference in maturation timing was greater, with most paedomorphic females maturing at two and metamorphic females at four or later. Whereas age of paedomorphic males did not exceed two years, it reached seven years in metamorphic males. The oldest paedomorphic female was five years old although the oldest metamorphic female was 10 years old (figure 1*a*).

Paedomorphs were smaller than metamorphs (males: $t_{319} = -9.91$, $p < 0.0001$; females: $t_{350} = -22.25$, $p < 0.0001$; figure 1*b*).

4. Discussion

While relatively similar in population A, age structures of paedomorphic and metamorphic newts greatly differed in population B. Paedomorphosis resulted in a retardation of somatic development in population A (retention of gill slits), but it resulted in an earlier sexual maturation in population B. Whereas mean body size did not differ between morphs in population A, paedomorphic newts proved to be smaller than metamorphs in population B.

Following Gould's typology (1977), paedomorphosis has to be qualified as neoteny in population A and as progenesis in population B. If these processes have been evidenced in different urodele species (Harris 1987; Kalezic et al. 1997; Ryan & Semlitsch 1998), the present study shows that both processes can produce paedomorphosis in natural populations of the same species.

According to Whiteman (1994), paedomorphosis may result in two ontogenetic pathways depending on the relative growth rates in aquatic and terrestrial habitats. When growth rate is higher in the aquatic habitat than in the terrestrial habitat (such as in fishless permanent lowland ponds surrounded by arid lands), selection for paedomorphosis is expected to result in an acceleration of sexual maturation in the fastest growing larvae. Such an acceleration of sexual maturation can lead to an increase in lifetime reproductive success as long as life span and age specific fecundity are not too much altered by subsequent reduction in body size. Early reproduction contributes to high intrinsic rate of natural increase, particularly after colonization of new habitats, catastrophe, and in case of competition with other species (Healy 1974; Roff 1992; Stearns 1992). When growth rate is lower in the aquatic habitat than in the terrestrial habitat (as suspected in high elevation ponds surrounded by favourable terrestrial habitats), paedomorphosis is expected to occur in the slowest growing individuals of a population, for which it represents a better solution than to delay maturation until reaching critical metamorphosis size ('best of a bad lot' hypothesis). In such a situation, fastest-growing larvae can take advantage of exploiting terrestrial habitats (Whiteman 1994).

Our data are in accordance with this hypothetical framework. In the high elevation site (population A), the small difference in age structure between paedomorphs and metamorphs suggests low variation in the length of their reproductive life. Such a similarity in age structures indicates that only few adult individuals switch from paedomorphic to metamorphic states. Late maturation probably results in stable demographic strategy, as shown by stability of the ratios of paedomorphs to metamorphs across years. The permanence of the lake is probably also a factor in the stability of the paedomorph : metamorph ratio.

For population B, shallow water, absence of fish, and low elevation are ecological conditions that are favourable to progenesis. These conditions probably also partly correspond to those required by the 'paedomorph advantage' hypothesis, although little is known about the suitability of the terrestrial habitats surrounding the pond for newt growth. The risks of drying up reduce the evolutionary expectancy of delaying maturation, as involved in neoteny. But, as shown by Semlitsch (1987) and Semlitsch & Wilbur (1989), the mere decrease of water level can induce metamorphosis even if the pond does not totally dry up. Moreover on the basis of Semlitsch's experiments (1987), high densities found for population B could also explain the large decrease of paedomorph proportion.

Ryan & Semlitsch (1998) hypothesized that salamanders that do not metamorphose may have more energy available for growth or sexual development. They demonstrated this point in an experimental framework in which ambystomatid paedomorphs matured earlier than metamorphs. We found the same results in a natural population of the Alpine newt, with the only difference that the paedomorphic and metamorphosed Alpine newts differed more in age at first reproduction than did ambys-tomatid salamanders. Indeed metamorphic Alpine newts usually require several years to mature (Miaud et al. 2000) whereas paedomorphs can mature at 1 year old (this study).

Our results support the hypothesis of multiple ontogenetic pathways depending on local environmental conditions (Whiteman 1994; Ryan & Sermlitsch 1998). However, identifying the ecological determinants of ontogenetic variation by field observations will remain a difficult task since several factors can act simultaneously (Svob 1965; Sprules 1974; Bizer 1978; Gabrion et al. 1978; Breuil 1992). Besides their low productivity, high elevation lakes are also large and deep ecosystems where large predators such as fish are often lacking unless artificially introduced. Such deep waters devoid of large predators provide conditions of spatial niche partitioning for the newts in allowing paedomorphic individuals to exploit the water column and the deepest zones (M. Denoël & P. Joly, unpublished data). Genetic variation between populations can also contribute to variation of the sensitivity to environmental factors. Italian populations present *apuanus* alleles that are suspected to influence the propensity of paedomorphosis. Such *apuanus* alleles have also been found in the French population we have studied (Breuil 1986).

Only estimations of age-specific survival, fecundity, and switching probability from paedomorphic to metamorphic morphs in each population would make it possible to model lifetime fitnesses of each alternative ontogenetic pathway, and thus to connect them to the selective pressures that act in each habitat (Roff 1992; Stearns 1992; Whiteman 1994). Other populations have to be investigated to generalize these results. As variation of reaction norm has been detected among populations, the question of the respective influences of environment and genotype on the expression of an ontogenetic pathway also represents an exciting perspective to the present work.

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