Evolutionary ecology of facultative paedomorphosis in newts and salamanders

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ABSTRACT

Facultative paedomorphosis is an environmentally induced polymorphism that results in the coexistence of mature, gilled, and fully aquatic paedomorphic adults and transformed, terrestrial, metamorphic adults in the same population. This polymorphism has been of interest to scientists for decades because it occurs in a large number of caudate amphibian taxa as well as in a large diversity of habitats. Numerous experimental and observational studies have been conducted to explain the proximate and ultimate factors affecting these heterochronic variants in natural populations. The production of each alternative phenotype is based on a genotype × environment interaction and research suggests that differences in the environment can produce paedomorphs through several ontogenetic pathways. No single advantage accounts for the maintenance of this polymorphism. Rather, the interplay of different costs and benefits explains the success of the polyphenism across variable environments. Facultative paedomorphosis allows individuals to cope with habitat variation, to take advantage of environmental heterogeneity in the presence of open niches, and to increase their fitness. This process is expected to constitute a first step towards speciation events, and is also an example of biodiversity at the intraspecific level. The facultative paedomorphosis system is thus ripe for future studies encompassing ecology, evolution, behaviour, endocrinology, physiology, and conservation biology. Few other systems have been broad enough to provide varied research opportunities on topics as diverse as phenotypic plasticity, speciation, mating behaviour, and hormonal regulation of morphology. Further research on facultative paedomorphosis will provide needed insight into these and other important questions facing biologists.

Key words: adaptation, amphibians, evolution, facultative paedomorphosis, heterochrony, polyphenism.

CONTENTS

I. INTRODUCTION

Facultative paedomorphosis (i.e. the potential for retention of juvenile traits in mature individuals) has roused the curiosity of biologists for more than a century. This phenomenon was first suspected by Cuvier (1828) who was reluctant to place the axolotl in the permanently branchiate salamanders, but its existence was first demonstrated by Dumerill (1866) at the Museum of Paris when he bred branchiate individuals of *Ambystoma mexicanum*. The metamorphosis of these axolotls into a form that was known as another salamander species provided the first evidence of developmental heterochrony between the sexual apparatus and the somatic tissues. For decades, such heterochronies in the development of caudate amphibians remained a zoological curiosity until a satisfactory theoretical framework was established to explore some explanatory hypotheses. The first studies were mechanistic and did not address evolutionary questions (Snyder, 1956; Sprules, 1974a; Gabrion, 1976). They considered facultative paedomorphosis to be a metamorphic failure caused by the detrimental effects of varied environmental factors. The environmental context of paedomorphosis proved to be so diverse that it became evident that the determinism of this trait was multifactorial (Semlitsch, 1987a; Breuil, 1992; Whiteman, 1994; Voss, 1995; Denoël, 2003a). Indeed, paedomorphosis occurs in such contrasting habitats as permanent mountain lakes surrounded by arid grounds and lowland temporary ponds surrounded by wet forests. The rise of modern evolutionary biology has opened new perspectives on this polymorphism, particularly within the framework of the evolution of phenotypic plasticity.

Phenotypic plasticity can result from heterochronic processes, consisting of a shift in the timing or rate of development of a functional set of biological traits relative to the development of the whole organism (Schlichting & Pigliucci, 1998). In animals with complex life cycles, heterochronic processes are expected to have profound consequences because of the interplay between larval and postmetamorphic traits that can lead to substantial differences between alternative morphotypes. Subsequently, such polyphenism can have a strong impact on the evolution of ecological communities (Gould, 1977; McKinney & McNamara, 1991).

Research suggests that genotypes able to produce alternative phenotypes would occur in heterogeneous environments in which each alternative can experience a higher fitness in the environment where the risks of suboptimal matching between resource availability and morpho-functional abilities are spread through phenotypic differentiation (Kaplan & Cooper, 1984; Gross, 1991; Skulason & Smith, 1995; Schlichting & Pigliucci, 1998). However, the evolution of polyphenism implies that the fitness gain drawn from the ecological specialisation of different phenotypes exceeds the cost of plasticity. Thus, polyphenisms are expected in environments where the scale of variability matches the adaptive potential of the developing phenotype (Levins, 1968). With regard to life history, polyphenisms are particularly expected in species with complex life cycles because the transition between habitats via metamorphosis is risky due to the lack of reliable information about the quality of the subsequent habitat (Wilbur & Collins, 1973; Werner, 1986). The ontogenetic pathway of species with complex life cycles is indeed characterized by the successive use of contrasting habitats (Nielsen, 1998). As a consequence, these species experience more environmental variation than single-habitat species. Selection for phenotypic plasticity is thus expected to be particularly strong in species with complex life cycles. The duration of each phase of a cycle should depend on the specific cost:benefit ratio (in terms of individual fitness) in each habitat.

Newts and salamanders exhibit a wide range of life cycles. At the extremes, some species can totally skip one stage and spend their whole life in only one habitat. This is the case in permanently gilled species (obligate paedomorphosis) that occupy aquatic habitats and of terrestrial species exhibiting direct development (Istock, 1967; Wilbur & Collins, 1973; Wilbur, 1996). Between these extremes, many salamanders exhibit a two-stage ontogenetic pathway with a larval aquatic stage and a terrestrial post-metamorphic stage (obligate metamorphosis) (Wilbur, 1980), while others exhibit facultative paedomorphosis (Duellman & Trueb, 1994). Each of these life cycles can be seen as a result of the interplay between costs and benefits experienced in both aquatic and terrestrial environments. Detrimental aquatic conditions (drying, crowding, low food availability, inbreeding, presence of predators) and unfavourable terrestrial situations (low humidity, absence of shelter, low food availability, high predation) may have driven species towards one of the basic life histories (Wilbur & Collins, 1973; Whiteman, 1994).

Paedomorphosis has been observed in fifty-seven species of newts and salamanders, distributed in nine of the ten recognized families. Four of them are only composed of obligatory paedomorphic species (Amphiumidae, Sirenidae, Proteidae, Cryptobranchidae). Such obligate paedomorphosis also occurs in a few species of Plethodontidae. Paedomorphosis is facultative in the Salamandridae, Ambystomatidae, Dicamptodontidae, Hynobiidae and some Plethodontidae. More than 10% of salamander species exhibit paedomorphic ontogenetic pathways (Semlitsch & Wilbur, 1989; Duellman & Trueb, 1994; Whiteman, 1994; Denoël, 2003a).

Interest in facultative paedomorphosis grew in the 1980s (e.g. Semlitsch & Gibbons, 1985; Harris, 1987; Semlitsch, 1987a; Semlitsch & Wilbur, 1989) after Wilbur and Collins (1973) published their growth model of metamorphosis timing. Most advances until the early 1990s were summarised by Whiteman (1994) who proposed alternative models to account for the variation of ontogenetic pathways among facultative paedomorphic species in natural and experimental conditions. Numerous authors have subsequently used facultative paedomorphosis as a model system in which to investigate the genetic bases and benefits of polyphenism in natural populations (Voss, 1995; Kalezic et al., 1996; Whiteman, Wissinger & Brown, 1996; Voss & Shaffer, 1997; Whiteman, 1997; Ryan & Semlitsch, 1998; Denoël & Joly, 2000, 2001; Denoël, Poncin & Ruwet, 2001b; Boorse & Denver, 2002; Denoël et al., 2002).

II. PROXIMATE MECHANISMS OF FACULTATIVE PAEDOMORPHOSIS

Cross-breeding experiments of paedomorphic and meta-morphic individuals produce Mendelian ratios, thus supporting a recessive gene coding for paedomorphosis (Tompkins, 1978). However, more recent intra- and interspecific crosses suggest a complex genetic basis (Harris *et al.*, 1990; Voss & Shaffer, 1997) that would differ among species (Shaffer & Voss, 1996; Voss *et al.*, 2003). Selection experiments (that remove metamorphic individuals at each generation) also support the hypothesis of high heritability of this trait, although the persistence of metamorphs in these experiments suggests an additive genetic basis (Semlitsch & Wilbur, 1989).

A variety of environmental factors have been experimentally shown to affect the expression of facultative paedomorphosis. Variation in density of conspecifics (Harris, 1987; Semlitsch, 1987*a*), desiccation rate (Semlitsch, 1987*a*; Semlitsch, Harris & Wilbur, 1990), temperature (Svob, 1965; Sprules, 1974*a*), and food availability (Sprules, 1974*a*; Voss, 1995; Ryan & Semlitsch, 2003) were shown to affect the proportions of larvae undertaking a paedomorphic pathway. Preliminary studies in amphibians suggest that stress hormones are the intermediate between environmental cues and metamorphosis (Denver, 1997; Boorse & Denver, 2002). On the other hand, paedomorphs are able to metamorphose at the adult stage (one-way reversible plasticity), at least in some species. The rate of reversion can be affected by such factors as desiccation (Denoël, 2003*c*), starvation (Denoël & Poncin, 2001) or thyroxine injection (Svob, 1965). However, the amount of time necessary to reach complete transformation of paedomorphic adults is often longer than that of larvae (Breuil, 1992; Denoël & Poncin, 2001), possibly because of the antagonist effect of sex-steroid hormones on thyroxine secretion (Denver, Glennemeier & Boorse, 2002). Experiments with standardized rearing conditions have shown that the sensitivity to environmental cues varies among populations (Semlitsch *et al.*, 1990). Such interplay between environment and genotype may account for the variation of the metamorph:paedomorph ratio across populations and species (Denoël *et al.*, 2001*a*).

III. ULTIMATE MECHANISMS OF FACULTATIVE PAEDOMORPHOSIS

(1) Resource partitioning

The evolution of facultative paedomorphosis results in a risk-spreading strategy that promotes a diversity of habitat uses within a single progeny. Paedomorphosis thus increases the probability of differentiation among offspring in resource use. When a resource that is exploited by one phenotype is depleted, the offspring exhibiting the other phenotype can potentially exploit an alternative resource. Such resource partitioning may increase fitness when high density increases resource competition among offspring
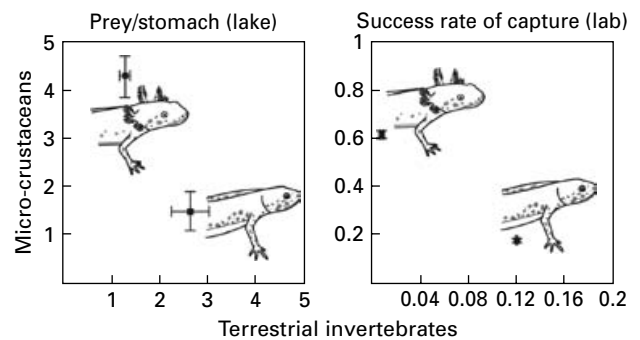

Fig. 1. Feeding habits (square-root transformed values) and performance of paedomorphic (drawn with gills) and metamorphic Alpine newts (modified from Denoël, 2004*a*; Denoël *et al.*, 2004). The two alternative morphs segregate in resource use according to opposed performance in prey capture: higher predation and capture success for plankton in paedomorphs and on terrestrial invertebrates that fell on the water surface in metamorphs. Values are means ± SE (feeding habits: N = 174 paedomorphs and 49 metamorphs; performance: N = 20 in each group).

(Skulason & Smith, 1995; Smith & Skulason, 1996; Denoël & Joly, 2001).

Paedomorphosis in newts and salamanders involves the retention of the larval feeding apparatus. As a consequence, the hydrodynamics of paedomorph foraging relies on unidirectional water flow: water is drawn into the mouth by suction and is then expelled backwards through the gill slits. By contrast, the closed gill slits in metamorphs leads to water being expelled through the mouth, resulting in a forward backflow (Lauder & Shaffer, 1993). The respective performance of each feeding morphology differs according to prey type. Whereas the unidirectional water flow system of the paedomorph oral apparatus is more efficient than the bidirectional flow of the metamorphs when foraging on aquatic prey (e.g., microcrustaceans) (Whiteman *et al.*, 1996; Denoël, 2004*a*), it is less efficient when foraging on terrestrial insects that are caught at the water surface (Denoël, 2004*a*) (Fig. 1).

Resource use in deep lakes where the two morphs coexist is consistent with laboratory observations. In Alpine newts (*Triturus alpestris*), paedomorphs forage mainly on plankton while metamorphs search for terrestrial invertebrates at the water surface (Denoël & Joly, 2001; Denoël & Schabetsberger, 2003; Denoël, Schabetsberger & Joly, 2004). In these populations, the two morphs either accrue similar caloric benefits or the paedomorphs have a higher food intake than the metamorphs, leading to better body condition (Denoël *et al.*, 2002). In addition to food partitioning, the two morphs also segregate according to microhabitat in this species, because the paedomorphs are particularly frequent in both the water column and the deepest parts of the lake, while metamorphs mainly live in shallower water near the shore and at the water surface (Denoël & Joly, 2001; Denoël & Schabetsberger, 2003; also true of some ambystomatids: Whiteman & Semlitsch, 2005). This habitat partitioning is congruent with breathing

mechanisms, as only paedomorphs have gills, and with food partitioning, as planktonic organisms are abundant in open and deep waters while terrestrial invertebrates predominate at both shore and surface microhabitats. Risk spreading through facultative paedomorphosis (*sensu* Werner, 1986) thus appears to be a valuable mechanism for explaining the plasticity of the ontogenetic pathway (Fig. 1). However, microhabitat use and food partitioning are only local components of the life cycles of the newts. We also have to consider processes that constrain the evolution of polyphenism at larger habitat scales. For example, the usual absence of dispersal in paedomorphs is costly since they cannot leave a pond to reach more productive habitats, or to avoid competition, predation (including cannibalism) or inbreeding (Whiteman, 1994; Whiteman, Wissinger & Bohonak, 1994; Whiteman *et al.*, 1996; Denoël, 2004*b*). Dispersal can bring advantages in populations that inhabit pond archipelagoes where the costs of movements from one pond to another are low. Optimal change of habitat is not always directly related to the hydroperiod, but rather appears to be dependent on the quality and quantity of food resources as temporary ponds can be favourable foraging habitats (Whiteman *et al.*, 1994; Whiteman *et al.*, 1996; M. Denoël & H. H. Whiteman, unpublished data).

Skulason & Smith (1995) predicted that the absence of interspecific competition should favour trophic polymorphisms. Available data on heterochronic newts and salamanders support this hypothesis. In most places inhabited by paedomorphic newts, no vertebrate competitors (e.g. other species of urodeles or fishes) were found although resource use by predatory invertebrates and newts might be similar (Denoël *et al.*, 2001*a*). When fishes are introduced, paedomorphs usually disappear rapidly from natural populations (Denoël, Dzukic & Kalezic, 2005). This could be due to competition, or to predation since fish have a strong impact on paedomorphic newt populations because of their aquatic lifestyle and pelagic behaviour (Denoël & Joly, 2001; Denoël & Schabetsberger, 2003). However, larvae might also avoid the paedomorphic ontogenetic pathway in the presence of fish as has been suggested by mesocosm experiments (Jackson & Semlitsch, 1993).

(2) Life-history traits

In newts and salamanders, paedomorphic phenotypes may be the product of different ontogenetic processes, the most frequent of them being progenesis and neoteny (Fig. 2). Progenesis consists of an acceleration of gonad development, which becomes functional at significantly younger ages than the usual onset of maturity in metamorphs. In contrast, neoteny results in slowing down the development of somatic structures, while the developmental rate of the gonads remains normal. Both processes lead to sexually mature individuals that retain larval somatic traits (Healy, 1974; Kalezic *et al.*, 1996; Denoël & Joly, 2000) (Fig. 2).

Similar to general predictions from models of heterochronic development (Gould, 1977; McKinney & McNamara, 1991; Klingenberg, 1998), progenetic paedomorphs are usually smaller than metamorphic adults, as the former can reach sexual maturity several years before the
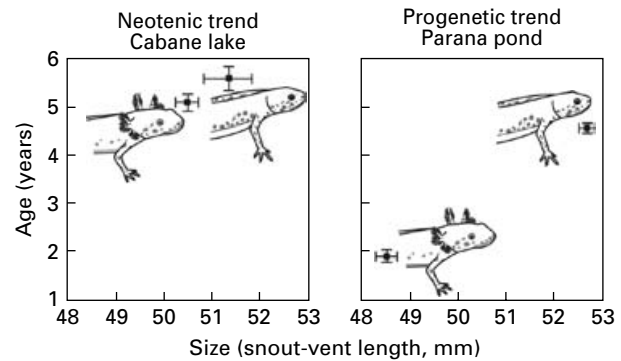

Fig. 2. Neotenic and progenetic processes in paedomorphosis (an example from Alpine newt populations). In progenesis, paedomorphs (drawn with gills) reach maturity at a younger age and smaller size than metamorphs. In neoteny, the pattern of sexual maturation and body growth remains unchanged in paedomorphs, but some parts of their soma develop slower than in metamorphs (modified from Denoël & Joly, 2000). Values are means ± SE (Cabane lake, age: N = 62 paedomorphs and 54 metamorphs, length: N = 105 and 47; Parana pond, age: N = 57 and 69, length: N = 273 and 400).

latter (Denoël & Joly, 2000). However, when the two morphs differ in age at maturity by only a few weeks or months, they are more similar in size, indicating that skipping metamorphosis would likely provide more energy for somatic growth (Ryan & Semlitsch, 1998). Age at maturity is thus probably an important target of natural selection for the evolution of facultative paedomorphosis (Ryan & Semlitsch, 1998).

Fecundity is a critical fitness component for many organisms, including facultative paedomorphic salamanders (Semlitsch, 1985, 1987*b*). In some cases, paedomorphic females exhibit lower fecundity than their metamorphic counterparts (Semlitsch, 1985; Kalezic *et al.*, 1996), but the reverse situation also exists (Semlitsch, 1985; Kalezic *et al.*, 1996; Rot-Nikcevic, Kalezic & Dzukic, 2000). Precocious oviposition by paedomorphic mole salamanders could result in their larvae gaining growth advantages over the larvae of metamorphs, which start breeding later in the season (Semlitsch, 1985). Early growth of the larvae may then translate into fitness benefits and higher survival later in life (Semlitsch, Scott & Pechmann, 1988; Ryan & Plague, 2004).

Maximization of individual reproductive success requires an optimal life cycle in terms of different traits, such as age at maturity and fecundity (Gross, 1985; Roff, 1992). Decreasing age at first reproduction or increasing the number of offspring at each breeding period will increase population growth rate, assuming no trade-offs with other life history traits (Roff, 1992). In newts and salamanders, paedomorphosis by progenesis has been observed in temporary ponds and neoteny in more permanent habitats (Healy, 1974; Denoël & Joly, 2000). This is in agreement with models predicting risk-spreading by precocious maturity in unstable habitats (Gould, 1977; Roff, 1992). However, because clutch size is closely related to body size in amphibians (Semlitsch, 1985), reproducing at a small size probably

reduces fecundity at first reproduction (Semlitsch, 1985). Nonetheless, because salamanders produce dozens to hundreds of eggs each year (Semlitsch, 1985; Kalezic *et al.*, 1996), even a small decrease in the age at maturity can have fitness consequences that are similar to a large increase in fecundity (Roff, 1992). By maturing just one year after hatching and more than one year before metamorphic adults, progenetic paedomorphs also benefit from an increased probability of breeding that results in rapid increase in fitness (Denoël & Joly, 2000).

(3) Sex-specific fitness

Sex-specific payoffs may influence the maintenance of polymorphism. By studying the time interval between breeding events in tiger salamanders, Whiteman (1997) showed that paedomorphic males bred more often than metamorphic males, while the reverse was true in females. This interaction effect promotes the maintenance of facultative paedomorphosis *via* sex-specific payoffs. The fact that paedomorphic females skip reproduction more often than metamorphic ones may be due to the low energy intake in permanent ponds and the high cost of egg production. The higher reproductive frequency in paedomorphic males is probably affected by their continued presence in breeding ponds, in contrast to metamorphic males, which depend on favourable climatic conditions (rainfall, temperature) during migration events from terrestrial overwintering sites. As predicted, the sex-ratio consistently differed between the two phenotypes with the males dominating in paedomorphs, and the females in metamorphs (Whiteman, 1997). The reverse of these sex ratios has been found in other populations, suggesting that the costs and benefits to each morph and sex vary by species and environmental conditions (Breuil, 1992; Whiteman, 1997; Ryan & Hopkins, 2000; Denoël, 2003*a*).

IV. PAEDOMORPHOSIS: A MODEL FOR SPECIATION?

Polymorphisms are suspected to be key steps in species evolution, particularly *via* sympatric differentiation where they promote reproductive isolation among morphs (Bush, 1994; Skulason & Smith, 1995; West-Eberhard, 2003). In this way, assortative mating within alternative morphs could make offspring of paedomorphs less likely to metamorphose (Semlitsch & Wilbur, 1989; Scott, 1993). Given differences in secondary sexual traits between morphs, sexual isolation might be expected. However, cross-breeding experiments in salamandrids showed that the two morphs interbreed successfully at an identical rate (Denoël *et al.*, 2001*b*). Additional observations and experiments suggest that this also occurs frequently in ambystomatids (Krenz & Sever, 1995; Whiteman, Gutrich & Moorman, 1999). In several species, the two morphs display similar behavioural patterns at similar frequencies (Whiteman *et al.*, 1999; Denoël *et al.*, 2001*b*; Denoël, 2002) or exhibit only slight differences in the content and timing of courtship (Krenz & Verrell, 2002).

They also use the same alternative tactics to attract females (Denoël, 2002, 2003*b*). This mating system differs from other polymorphisms in which morphs display alternative tactics or strategies with equal or different fitness payoffs (Gross, 1991, 1996; Fu, Neff & Gross, 2001). Sexual compatibility promotes significant gene flow between morphs, and impedes differentiation as long as the environmental pressures do not change (Denoël *et al.*, 2001*b*; Krenz & Verrell, 2002). Thus even though facultative paedomorphosis is adaptive because of the flexibility it affords offspring, breeding studies suggest that this polymorphism is unlikely to lead to future speciation events.

Yet, in some salamander populations sexual isolation might occur because paedomorphs breed weeks or months earlier than metamorphs, thus leading to assortative mating (Whiteman & Semlitsch, 2005). This situation might be reinforced by the low mating activity of females after first insemination (Krenz & Sever, 1995). Spatial segregation of the two morphs in large ponds can also promote assortative mating among morphs (Whiteman & Semlitsch, 2005). In these cases, temporal and spatial differences can lead to partial reproductive isolation, such that gene flow is reduced among certain morph-sex combinations (Whiteman & Semlitsch, 2005).

Isolated permanent lakes or springs offer opportunities for divergence by allopatric speciation, particularly if the terrestrial morph is counter-selected. The spatial distribution of Mexican lakes where paedomorphic species of ambystomatid salamanders live provides such an ecological framework because they are isolated from each other by considerable amounts of inhospitable terrestrial habitat. As a consequence, paedomorphic populations of the different lakes evolve independently (Shaffer, 1993). A similar situation occurs in *Eurycea* salamanders (Plethodontids) which inhabit isolated springs on the Edwards Plateau in Texas (Chippindale *et al.*, 2000). Obligatory paedomorphosis in some amphibian families might have arisen in such situations where life on land is counter-selected leading to a fully aquatic lifestyle. Even in less isolated systems, genetic differentiation of developmental mechanism was found in ambystomatid salamanders from South Carolina (Harris *et al.*, 1990; Semlitsch *et al.*, 1990). These results indicate that differentiation of developmental programs can occur quickly when gene flow among populations is low.

V. MODELS OF PAEDOMORPHOSIS

Both predictive and diversifying models of phenotypic plasticity have been proposed to account for the mechanisms leading to environmentally-induced phenotypes (Kaplan & Cooper, 1984; Menu & Debouzie, 1993). According to predictive plasticity models, phenotypes are induced following the perception of environmental indices that reliably inform the individual of future environmental conditions (Menu & Debouzie, 1993). Paedomorphic responses to permanent water and low density support this model (Harris, 1987; Semlitsch, 1987*a*). By undergoing metamorphosis following a decrease in water level and/or an increase
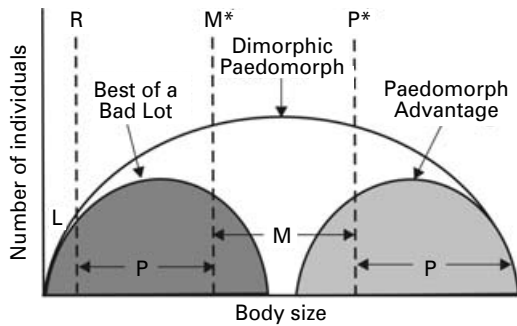
Fig. 3. Three ecological models of paedomorphosis (modified from Whiteman, 1994): the Best of a Bad Lot (dark shaded semi-circle), the Paedomorph Advantage (light shaded semi-circle) and the Dimorphic Paedomorph Hypothesis (open semi-circle). R: minimum size for sexual maturity, M^*: minimum size for metamorphosis, P^*: minimum size for paedomorphosis through the Paedomorph Advantage model, L: larval stage, P: paedomorphic stage, M: metamorphic stage.

in density, both larvae and, in some cases, paedomorphic adults escape an aquatic environment that is becoming unfavourable. Such a transition generally occurs just before the pond dries, allowing individuals to optimize the benefit of their aquatic habitat (Semlitsch *et al.*, 1988; Denoël, 2003 *c*). Food availability can also influence the ontogenetic pathway, but *via* a more complex mechanism. Whereas the frequency of metamorphosis increases in adult paedomorphs as aquatic food resources become scarce (thus supporting the predictive plasticity hypothesis) (Denoël & Poncin, 2001), food limitation can delay metamorphosis in larvae (Sprules, 1974 *a*; Voss, 1995; Ryan & Semlitsch, 2003).

Whiteman (1994) modified the Wilbur–Collins metamorphosis model (Wilbur & Collins, 1973) to create three hypotheses for the production and maintenance of facultative paedomorphosis according to habitat quality (Fig. 3). The Paedomorph Advantage (PA) mechanism corresponds to the basic model of Wilbur and Collins (1973). It predicts that large, fast-growing animals (larger than P*, the minimum size for paedomorphosis in Fig. 3) in good growing habitats (where growth rate is high) become paedomorphic, while animals smaller than P* metamorphose to escape competition with larger paedomorphs. By contrast, the Best of a Bad Lot (BOBL) hypothesis predicts the reverse solution in poor habitats (low growth conditions): the larger larvae (>M*, the minimum size for metamorphosis) metamorphose, while the smallest ones (between R, the minimum size for sexual maturity, and M*) keep a larval somatic state and become reproductively mature. Finally, the Dimorphic Paedomorph (DP) hypothesis suggests that paedomorphosis results from both mechanisms according to the local conditions experienced by each individual.

These predictions assume that growth rate is a key integrative parameter, and that body size is related to fitness. For example, the PA hypothesis suggests that fast-growing larvae in rich habitats experience a fitness advantage in this habitat. By contrast, the BOBL hypothesis predicts that larvae that cannot reach a sufficient size for metamorphosis take advantage of early maturity as a stopgap solution.

Evidence for both hypotheses in the same population would support the DP.

Assuming a strong relationship between fitness parameters and body size (Semlitsch, 1985, 1987 *a*), the model predicts that paedomorphs produced through a PA mechanism would have higher fitness than metamorphs (e.g. in fecundity or mating success), while the reverse would be true when paedomorphs are produced through a BOBL mechanism (although there might be a decrease in age at first reproduction). The DP suggests that mean fitness might not differ between morphs within a population, but the variance in fitness should be greater in paedomorphs than metamorphs because paedomorphs are produced through two mechanisms that differ strongly in their fitness payoffs.

Although a number of studies have supported both the PA and BOBL hypotheses (Whiteman, 1994; Whiteman *et al.*, 1996; Denoël & Joly, 2000; Ryan & Semlisch, 2003; J. M. Doyle & H. H. Whiteman, unpublished data), by far the most support has been found for PA, perhaps due in part to the good growing conditions in which many studies have been conducted. It is clear from experimental and observational studies of larval growth patterns that both mechanisms can operate to produce paedomorphs in nature; what is less clear is how the fitness consequences of each morph correspond to the hypotheses, if they do so at all. Because current studies have only addressed fitness components and not lifetime reproductive success (LRS), our ability to evaluate this question may have to wait until more complete LRS analyses of facultatively paedomorphic species are performed.

VI. CONCLUSIONS AND PERSPECTIVES

(1) Facultative paedomorphosis occurs in habitats as diverse as deep oligotrophic permanent alpine lakes and small eutrophic temporary ponds, surrounded by arid areas as well as by wet forests (Healy, 1974; Sprules, 1974 *b*; Breuil, 1992; Whiteman, 1994; Denoël *et al.*, 2001 *a*). The diversity of these environments, and the animals within them, has made it challenging to create a satisfactory explanatory framework. By identifying the multiple pathways that can drive an individual toward paedomorphosis, recent studies now make it possible to draw a conceptual framework for explaining the evolutionary success of facultative paedomorphosis in a great diversity of environments (Semlitsch, 1987 *b*; Whiteman *et al.*, 1996; Voss & Shaffer, 1997; Whiteman, 1997; Ryan & Semlitsch, 1998; Denoël & Joly, 2000, 2001; Denoël *et al.*, 2002).

(2) Although many studies have been conducted to explain the existence and maintenance of polymorphisms, and particularly facultative paedomorphosis, the mechanism(s) of its expression remains poorly understood (Denver *et al.*, 2002; Voss *et al.*, 2003).

(3) New methods, such as candidate gene analysis, that have recently been used to determine the alleles involved in the timing of metamorphosis will increase our knowledge in the area (Voss *et al.*, 2003).

(4) New research should also focus on the molecular transcription of signals that induce larvae to become

paedomorphs and not metamorphs. Stress hormones are obvious key targets for the mediation between environmental cues and resulting developmental pathways (Boorse & Denver, 2002), yet little work has focused on the hormonal basis of paedomorphosis.

(5) Recent work suggests that sex should also be incorporated into models to explain the maintenance of polymorphism (Whiteman, 1997). Further studies, in particular those dealing with hormones, should take sex effects into account as sex hormones act on the processes of metamorphosis (Denver *et al.*, 2002).

(6) Finally, fluctuations in natural populations of paedomorphic newts and salamanders need to be explained in regard to natural and anthropogenic causes, including how the polymorphism might affect the frequency, amplitude, and metapopulation effects of fluctuation (Denoël *et al.*, 2005; Whiteman & Wissinger, 2005). Rapid environmental changes in systems composed of permanent and drying ponds are of particular interest (Healy, 1974; Kalezic & Dzukic, 1985; Breuil, 1992; Whiteman *et al.*, 1996).

(7) The facultative paedomorphosis system is thus ripe for future studies encompassing ecology, evolution, behaviour, endocrinology, physiology, and conservation biology. Few other systems have been broad enough to provide varied research opportunities on topics as diverse as phenotypic plasticity, speciation, mating behaviour, and hormonal regulation of morphology. Further research on facultative paedomorphosis is sure to provide needed insight into these and other important questions facing biologists.

VII. ACKNOWLEDGEMENTS

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