The Evolution of Paedomorphosis in Salamanders

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Heterochrony, defined as changes to the ancestral rate of development in different parts of an organism, greatly impacts the final adult morphology. It is believed to be a driving force in both macro- and microevolutionary processes (Denoël and Joly, 2008; Denoël et al., 2019). The three key drivers behind this observation are the variations in growth onset, offset, and rate. The interplay between these factors gives rise to paedomorphosis, a phenomenon commonly studied in salamanders due to their extreme diversity of species and morphology (Fabre et al., 2020). Unlike most amphibians, who undergo metamorphosis to mature from aquatic larvae into terrestrial adults, paedomorphic salamanders preserve larval traits into adulthood and retain the ability to metamorphose. This review paper uses the *Paedomorph Advantage Hypothesis*, the most widely supported explanation for the evolution of paedomorphosis, to explore the adaptive significance of this trait in salamanders.

The *Paedomorph Advantage Hypothesis* predicts that overall, paedomorphs should have higher fitness than metamorphs in favorable aquatic environments (Whiteman, 1994). In this hypothesis, paedomorphs refer to facultative paedomorphs: individuals capable of metamorphosis or paedomorphosis depending on environmental conditions experienced as a larva. This form of extreme phenotypic plasticity contrasts with fixed developmental phenotypes exhibited by metamorphs, where one metamorphoses regardless of the environmental conditions. Consequently, natural selection should favor genotypes that enable flexible developmental responses to the changing environment. In favorable environments characterized by lower population density and higher resource availability, paedomorphs usually remain in the waters. On the contrary, unstable aquatic environments encourage larvae to metamorphose and transition into a more hospitable terrestrial lifestyle. Paedomorph's dynamic conformation to environmental conditions provides several advantages, particularly in reproductive success and ecological specialization, discussed below.

Early sexual maturity and shortened generation time are a major contributor to paedomorph's reproductive fitness. Metamorphosis demands a tremendous amount of time and energy devoted to rearranging morphological traits. Paedomorphs altogether bypass this process and redirect resources toward earlier reproduction and higher-quality gametes (Ryan and Semlitsch, 1998). For example, red-spotted newts (*Notophthalmus viridecens viridecens*) who remain paedomorphs reach reproductive age at two, whereas metamorphosed individuals only reach this stage three to seven years later (Healy, 1974). Upon attaining an early reproductive age, paedomorphs can reproduce whenever environmental conditions allow, whereas metamorphs' migration to breeding sites is constrained by abiotic factors (i.e. temperature, humidity, and precipitation). When breeding migration is delayed, paedomorphs may complete reproduction before the arrival of metamorphs. Consequently, overlap in breeding territories and competition for resources are minimized. In the mole salamander (*Ambystoma talpoideum*), mating and hatching of some paedomorphic larvae occurred before the arrival of metamorphic adults (Ryan and Semlitsch, 1998). Such low-density habitats confer higher offspring survival and growth advantages, and these offspring will grow up to be more high-performing. This flexible reproductive strategy therefore contributes to an overall higher reproductive fitness.

However, reproductive success alone does not fully explain paedomorph's adaptive significance. A second dimension of the *Paedomorph Advantage Hypothesis* is supported by the *Trophic Advantage Hypothesis*. This hypothesis proposes that paedomorphs' diverse morphology enhances exploitation of unused resources and adaptation to unique ecological niches (Whiteman, 1994). Without restraints needed for both aquatic and terrestrial adaptation, paedomorphs exhibit greater morphological variability specialized for aquatic lifestyles. Indeed, they display a dramatic increase, up to 18-times higher, in the evolutionary rates of the adult body form compared to metamorphs (Bonett and Blair, 2017). This morphological diversity offers competitive advantages: paedomorphs can acquire resources unattainable for metamorphs and colonize new ecological niches (Frédérich et al., 2017; Lejeune et al., 2021). For instance, Alpine newts (*Triturus alpestris*) inhabit cold ponds up to 8,000 feet above sea level in the European Alps. They primarily feed on plankton—a resource inaccessible to metamorphs who mostly forage near the shorelines and surface of water. By exploiting deep-water habitats and specialized diets, paedomorphs reduce interspecific competition through resource partitioning (Denoël and Joly, 2008). Thus, the *Trophic Advantage Hypothesis* reinforces the adaptive significance of paedomorphosis in a stable aquatic environment.

While the hypotheses discussed above illustrate adaptive advantages, the *Best of Bad Lot Hypothesis* argues that paedomorphosis may not always be adaptive: it is the backup mechanism for surviving in poor aquatic conditions (Whiteman, 1994). Such conditions are opposite to that in the *Paedomorph Advantage Hypothesis*, and they include higher density and lower resource availability relative to the terrestrial environment. Under these circumstances, larger and faster-growing larvae can metamorphose to escape the waters. Smaller larvae do not grow fast enough to reach the critical body size to metamorphose, and are then forced to mature as paedomorphs in the water (Whiteman et al., 2011). Therefore, paedomorphosis may present the best option when metamorphosis is physically not possible. This phenomenon is observed in *Ambystoma tigrinum*, a species distributed across varying elevation levels. Lower-elevation populations experience warmer climates and

resource-abundant conditions that support larger larvae size and metamorphosis. At higher elevations, cooler temperatures and scarce food levels restrict growth rate. As a result, the larvae are smaller and are typically forced to mature as paedomorphs (Bizer, 1978). This phenomenon is associated with reduced lifetime fecundity, as demonstrated in the mole salamanders (*Ambystoma talpoideum*). In a population of forced paedomorphs, they produced fewer eggs than terrestrial metamorphs of the same age (Semlitsch, 1985). In this scenario, early reproduction compensates for decreased fecundity. This contrasts with the *Paedomorph Advantage Hypothesis*, in which early reproduction ensures higher-quality offspring, rather than to make up for reduced reproductive fitness.

In conclusion, the *Paedomorph Advantage Hypothesis* and the *Best of Bad Lot Hypothesis* provide a framework for explaining the paedomorph's survival mechanism in both favorable and unfavorable aquatic conditions. In favorable environments, paedomorphosis is an advantageous lifestyle that encourages early reproduction and flexible adaptation for unused resources. In contrast, when metamorphosis is unattainable in unfavorable habitats, this trait fulfills the fundamental survival and reproductive demands. Ultimately, paedomorphosis reflects salamanders' versatile ability to adjust to changing environments.

References

Bizer, J. R. (1978). Growth rates and size at metamorphosis of high elevation populations of *Ambystoma tigrinum*. *Oecologia*. **34**, 175-184.

Bonett, R. M. and Blair, A. L. (2017). Evidence for complex life cycle constraints on salamander body form diversification. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 9936-9941.

Denoël, M., Drapeau, L., Oromi, N. and Winandy, L. (2019). The role of predation risk in metamorphosis versus behavioral avoidance: a sex-specific study in a facultative paedomorphic amphibian. *Oecologia*. **189**, 637-645.

Denoël, M. and Joly, P. (2008). Adaptive significance of facultative paedomorphosis in *Triturus alpestris* (Amphibia, Caudata): resource partitioning in an alpine lake. *Freshw. Biol.* **46**, 1387-1396.

Fabre, A., Bardua, C., Bon, M., C, J., Felice, R. N., Streicher, J. W., Bonnel, J., Stanley, E. L., Blackburn, D. C. and Goswami, A. (2020). Metamorphosis shapes cranial diversity and rate of evolution in salamanders. *Nat. Ecol. Evol.* **4**, 1129-1140.

Frédérich, B., Santini, F., Konow, N., Schnitzler, J., Lecchini, D. and Alfaro, M. E. (2017). Body shape convergence driven by small size optimum in marine angelfishes. *Biol. Lett.* **13**, 20170154.

Healy, W. R. (1974). Population consequences of alternative life histories in *Notophthalmus v. viridescens. Copeia*. **1974**, 221-229.

Lejeune, B., Bissey, L., Didaskalou, E. A., Sturaro, N., Lepoint, G. and Denoël, M. (2021). Progenesis as an intrinsic factor of ecological opportunity in a polyphenic amphibian. *Funct. Ecol.* **35**, 546-560.

Ryan, T. J. and Semlitsch, R. D. (1998). Intraspecific heterochrony and life history evolution: Decoupling somatic and sexual development in a facultatively paedomorphic salamander. *Proc. Natl. Acad. Sci. U.S.A.* **95**, 5643-5648.

Semlitsch, R. D. (1985). Reproductive strategy of a facultatively paedomorphic salamander *Ambystoma talpoideum*. *Oecologia*. **65**, 305-313.

Whiteman, H. H. (1994). Evolution of Facultative Paedomorphosis in Salamanders. *Q. Rev. Biol.* **69**, 205-221.

Whiteman, H. H., Wissinger, S. A., Denoël M., Mecklin, C. J., Gerlanc, N. M. and Gutrich, J. J. (2011). Larval growth in polyphenic salamanders: making the best of a bad lot. *Oecologia*. **168**, 109-118.