

Short- and long-term advantages of an alternative ontogenetic pathway

MATHIEU DENOËL^{1,*}, FRÉDÉRIC HERVANT², ROBERT SCHABETSBERGER³ and PIERRE JOLY²

¹Laboratory of Ethology and Animal Psychology, University of Liège, 4020 Liège, Belgium

²Laboratory of Ecology of Fluvial Hydrosystems, Claude Bernard University of Lyon, 69622 Villeurbanne, France

³Zoological Institute, University of Salzburg, 5020 Salzburg, Austria

Abstract

We documented hypotheses on the evolution of developmental heterochronies by estimating short- and long-term advantages of alternative morphs. In this respect, we compared food energy intakes and body condition between paedomorphic and metamorphic Alpine newts (*Triturus alpestris*, Caudata, Amphibia) in four populations. Because we found a strong correlation between fat reserves and body condition, we used this last parameter as an indicator of long-term gains. In all studied sites, paedomorphic females showed higher body condition than metamorphic ones. Paedomorphic males were also at advantage in two populations. Paedomorphs exhibited higher energy intakes than metamorphs in two populations and similar gains in two others. Our results support unifying theories that predict the occurrence of facultative paedomorphosis in varied habitats as paedomorphs exhibited better energy balance than metamorphs. This work shows the need for considering integrative parameters such as body condition in the comparative study of performances when studying developmental heterochronies.

© 2002 The Linnean Society of London

Additional keywords: facultative paedomorphosis; heterochrony; polymorphism; fat reserves; body condition; energy intake; habitat; newt

Introduction

Developmental heterochronies such as paedomorphosis (retention of ancestral subadult traits in adult individuals) are suspected to play important roles in micro- and macro-evolutionary processes (Gould, 1977; McKinney & McNamara, 1991). In this respect, heterochronic modifications of ontogenetic pathways are assumed to produce new morphotypes able to occupy adaptive peaks that differ from those of ancestral morphs (McKinney & McNamara, 1991). Developmental heterochronies originate in processes of phenotypic plasticity. Plasticity is an adaptive response to environmental variability that allows a genotype to cope with a broader range of ecological conditions, particularly in heterogeneous and unstable habitats (Bradshaw, 1985; Schlichting, 1986; Scheiner, 1993). Because plasticity produces phenotypic variation which is exposed to natural selection, the interplay between plasticity and selection may secondarily lead to differentiation of innovative life history tactics such as the appearance of new morphotypes able to build new ecological niches. However, only few empirical studies (Stanley, 1972; McNamara, 1983; McKinney & McNamara, 1991) actually support such theoretical considerations.

Heterochronic processes have been described in such different groups as mammals (Shea, 1983),

birds (Livezey, 1992), amphibians (Wilbur & Collins, 1973), fishes (Meyer, 1987), insects (Leclerc & Regier, 1990), molluscs (Stanley, 1972), brachiopods (McNamara, 1983), and hydroids (Blackstone & Buss, 1993). Despite occurring frequently, the evolution of new morphotypes has not given rise to many explanatory models (Schlichting & Pigliucci, 1998). Wilbur & Collins (1973) and Whiteman (1994) have proposed optimality models to explain and predict paedomorphosis occurrence in newts and salamanders. In these amphibians, the differentiation of several families (Proteidae, Necturidae and Sirenidae) is suspected to have resulted from paedomorphic processes. Facultative paedomorphosis is commonly observed in present populations of newts or salamanders that are composed of both paedomorphic and metamorphic individuals. In such populations, paedomorphic individuals retain most of the larval somatic characters (e.g. gills and gill slits) when reaching sexual maturity (Gould, 1977; Semlitsch & Wilbur, 1989).

Facultative paedomorphosis makes it possible to investigate cost–benefit implications of heterochronic plasticity in natural populations (Whiteman, 1994; Ryan & Semlitsch, 1998). Evolutionary models primarily assume that metamorphosis is bypassed when the aquatic habitat is more favourable than the terrestrial environment (Wilbur & Collins, 1973; Werner, 1986; Whiteman, 1994). Fast growing larvae would then mature before undergoing me-

* Correspondence. E-mail: Mathieu.Denoel[a]ulg.ac.be

Table 1. Description of the sites studied. UTM: Universal Transverse Mercator coordinates; volume and depth are maximum values

Site	Locality	Country	UTM	Altitude (m)	Volume (m ³)	Depth (m)	Surroundings
A	Lac de la Cabane	France	32TKQ91	1950	25000	7.5	Alpine pastures and coniferous forest
B	Parana	Italy	32TNQ60	600	100	0.7	Pastures, close to deciduous forest
C	Drakolimni-Tymphi	Greece	34SDK82	2000	16000	3.7	Alpine pastures
D	Drakolimni-Smolikas	Greece	34TDK93	2140	6000	4.9	Alpine pastures

tamorphosis, thus taking advantage of the aquatic habitat in increasing the length of their reproductive lifetime ('paedomorph advantage hypothesis'). Nevertheless, paedomorphosis also occurs in habitats that do not fit this pattern. Whiteman (1994) therefore proposed an alternative model, which predicts that paedomorphosis is the only ontogenetic outcome for the slowest-growing larvae in an unfavourable aquatic habitat where they cannot support the costs of metamorphosis before wintering ('best-of-a-bad-lot hypothesis'). The early maturation of paedomorphs (Ryan & Semlitsch, 1998; Denoël & Joly, 2000) and the high incidence of paedomorphosis in permanent waters where density is low (Harris, 1987; Semlitsch, 1987; Semlitsch & Wilbur, 1989) and prey availability high (Denoël & Poncin, 2001) support the first hypothesis. In contrast, the slowest growth of paedomorphs in permanent lakes supports the alternative hypothesis (Whiteman, Wissinger & Brown, 1996). High frequency of paedomorphic newts or salamanders in cold, high elevation lakes (Sprules, 1974; Bizer, 1978) might also be consistent with this hypothesis because larval growth is slowed down by low temperatures and metamorphosis is constrained by a short active period. In populations with variations in body size, the best of a bad lot hypothesis can explain how paedomorphosis can appear and persist in populations that experience harsh aquatic conditions. In addition, advantages gained later in life could favour the larvae involved in such an ontogenetic pathway as such phenotype-environment interactions may influence fitness in a great variety of ways. In the present paper we will suppose that the advantages of paedomorphosis lie (i) in the avoidance of the costs due to habitat switching and migration; (ii) in the access to new feeding resources that promote niche partitioning, thus reducing competition between morphs (Fasola, 1993; Whiteman et al., 1996; Denoël & Joly, 2001a,b).

Measures of short- and long-term cost-benefit balance of each alternative ontogenetic pathway are needed to evaluate the relevance of these hypotheses and to identify the mechanisms underlying the maintenance of heterochronic polymorphisms in natural populations. In this respect, the aim of this study was to compare lipid contents, body condition, and food energy intakes of syntopic paedomorphic and metamorphic Alpine newts in several populations.

Material and methods

Study sites

We studied four populations of the Alpine newt *Triturus alpestris* (Laurenti, 1768) located in France, Italy and Greece (Table 1). These aquatic sites were selected because they contain large populations of newts composed of the two heterochronic morphs. In all these sites, paedomorphs and metamorphs can be found during the whole reproductive period, which lasts a few months after winter thawing.

Sexual activity and egg laying occur synchronously in the two morphs for a few months (Miaud, 1990; Denoël et al., 2001a; Denoël, 2001). Paedomorphs outnumbered metamorphs in sites A and D, but the inverse was observed in sites B and C (Denoël, 2001).

Sampling and identification

Adult newts of both morphs were sampled in water by dip-netting from a boat, from the shore, and by scuba diving. Samples were collected during the beginning of the active period: June 1997 at site A, April 1997 at Site B and July 1999 at sites C and D. Sex and maturity stage were established according to the shape of the cloaca (swollen and smooth in males; small, long and striated in females; a simple slit in juveniles). Morph type was determined by presence or absence of gills and gill slits in adult newts (Denoël, Poncin & Ruwet, 2001b).

Body condition, metabolite assays and energy intakes

Immediately after capture, we anaesthetized the newts with phenoxy-ethanol (immersion in a 0.5-g/L solution). We then measured snout-vent to the nearest 1 mm and body weight to the nearest 0.1 g. Body condition was estimated by the residuals of the regression of log(body mass) on log(snout-vent length) (Jakob, Marshall & Uetz, 1996). Samples consisted of 223 newts at site A, 253 at site B, 180 at site C and 422 at site D.

We extracted stomach contents by stomach flushing and stored them separately in 4% formaldehyde (223 newts at site A, 254 at site B, 184 at site C and 329 at site D). Prey were identified and measured (total length). Their energy content (in Joules) was then estimated using specific relationships between size and weight, and specific relationships between weight and energy contents (Cummins & Wuicheck, 1971; Jorgensen, 1979; P. Joly, unpublished data). Metabolite assays were established to validate measures of condition as an indicator of fat reserves and thus of long-term gains. To estimate body contents of stored fat, we deep-froze nine females of each morph from site A in liquid nitrogen and stored them in closed vials at -30 °C. The frozen tissues of the whole animals were homogenized (using an Ultra-Turrax) in 60 mL of 2 : 1 chloroform/methanol solution. Whole body total lipids and triglycerides were extracted from tissues according to Barnes & Blackstock (1973) and Hervant, Mathieu & Durand (2001). We weighed total lipids in tarred vials, and measured the contents in triglycerides using specific test-combinations (Boehringer-Mannheim). All assays were performed in a recording spectrophotometer (Beckman DU-6) at 25 °C. The accuracy of each analysis had been previously tested by assaying the samples with and without an added internal standard. The sensitivity of the assays was approximately 1 µmol g⁻¹ dw for all metabolites.

Table 2. Comparisons of residuals of the linear regression of log (mass) on log (snout–vent) length between the two Alpine newt morphs at each site studied

	Population	Paedomorphs		Metamorphs		<i>t</i> -test	<i>P</i>
		Mean residual	SE	Mean residual	SE		
Females	A	0.009	0.005	– 0.034	0.008	$t_{127} = 4.248$	<0.001
	B	0.011	0.007	– 0.012	0.007	$t_{139} = 2.263$	<0.05
	C	0.016	0.006	– 0.016	0.010	$t_{89} = 2.750$	<0.01
	D	0.025	0.004	– 0.027	0.005	$t_{233} = 8.053$	<0.01
Males	A	– 0.004	0.006	0.014	0.010	$t_{92} = -1.483$	0.14
	B	0.008	0.005	– 0.005	0.004	$t_{110} = 1.964$	0.05
	C	0.020	0.007	– 0.021	0.011	$t_{87} = 3.209$	<0.01
	D	0.031	0.005	– 0.030	0.006	$t_{185} = 7.305$	<0.001

We performed *t*-tests to compare lipid/triglyceride contents and body condition between paedomorphs and metamorphs. A two-way anova was performed to test the respective effects of morph, sex, and their interaction on energy values (Zar, 1996). Post-hoc LSD tests were computed to compare energy values between morphs within each sex (Day & Quinn, 1989). All statistical tests were two-tailed. Data were log-transformed to assure linearity between variables and to fit the conditions of anovas and regressions. Logarithms (base 10) of lipid, triglyceride and energy intake values were weighted by the logarithm of snout–vent length to get values independent of the size of the individuals. We accepted a maximum Type 1 error risk of 0.05.

Results

Lipid contents (log[lipid mass]/log[snout–vent length]) were significantly higher in paedomorphs (mean \pm SE = -0.606 ± 0.020 g) than in metamorphs (mean \pm SE = -0.754 ± 0.018 g) ($t_{16} = 5.363$, $P < 0.001$). Triglyceride contents were significantly higher in paedomorphs (mean \pm SE = 0.552 ± 0.026 mmol) than in metamorphs (mean \pm SE = 0.353 ± 0.019 mmol) ($t_{16} = 6.177$, $P < 0.001$).

Each regression of lipid and triglyceride contents on body condition was significant ($Y = -0.680 + 0.879x$, $r = 0.723$, $t_{16} = 4.190$, $P < 0.001$ and $Y = 0.453 + 1.056x$, $r = 0.674$, $t_{16} = 3.653$, $P < 0.01$, respectively), allowing the use of body condition as a suitable predictor of lipid and triglyceride contents.

The slopes of the regression of mass on snout–vent length did not significantly differ between the two morphs within sex and within population (*t*-test), except for males at site D ($t_{183} = 3.111$, $P < 0.01$; Fig. 1). At this site, the slope of the regression was higher in metamorphs than in paedomorphs. Body condition scores were significantly higher in paedomorphs than in metamorphs for each site and sex (*t*-test, $P < 0.05$), but no significant difference was found for males at sites A and B ($P = 0.14$ and $P = 0.05$, respectively; Table 2, Fig. 1).

Morph had an overall significant effect on the energy content of the stomach at all sites except site D, with higher energetic contents of the stomach in paedomorphs (Table 3). Sex had a significant effect only at site B, and the interactions between morph and sex were never significant. Paedomorphic females had stomach contents of significantly higher energetic value than metamorphic females at sites B and C. In males, significantly higher energy intakes were only detected in paedomorphs at site B (Fig. 2).

Discussion

Because of the positive relationships between fat contents (triglycerides and whole lipids) and body condition, body condition can be used as a reliable estimation of the storage of biological fuels. The amount of biological fuels has been proven to be positively correlated with clutch size (Scott & Fore, 1995) and survival (Jiang & Claussen, 1992; Pinder, Storey & Ultsch, 1992) in urodele amphibians. Paedomorphic newts of both sexes exhibited higher body condition than metamorphic newts at all sites, except males at sites B and C. The paedomorphic pathway thus appears to provide a significant advantage regardless of the varied characteristics of the aquatic and terrestrial habitats (elevation, area, depth, and types of surrounding terrestrial habitats).

When the stomach energy contents significantly differed, paedomorphic newts were at an advantage, with higher energy values in paedomorphs than in metamorphs. This occurred in two populations for females and in one population for males. Differences in energy content may be due to variation in prey selectivity for paedomorphs which foraged more frequently on zooplankton, and less frequently on terrestrial invertebrates than did metamorphs (Denoël & Joly, 2001a). Despite the fact that the sampled stomach contents represent only snapshots of the diet of the newts, the analysis of their energy values converges with the results on body condition and body fat contents in showing the advan-

Table 3. Two-way anova on the energy content of the stomach (weighted by snout–vent length) of the Alpine newts

Population	Source	d.f.	MS	<i>F</i>	<i>P</i>
A	Morph	1	0.266	4.074	<0.05
	Sex	1	0.036	0.547	0.45
	Morph \times sex	1	0.056	0.861	0.35
	Error	219	0.065		
B	Morph	1	2.161	13.680	<0.001
	Sex	1	1.097	6.947	<0.01
	Morph \times sex	1	0.018	0.116	0.73
	Error	250	0.158		
C	Morph	1	1.175	7.588	<0.01
	Sex	1	0.153	0.990	0.32
	Morph \times sex	1	0.488	3.158	0.07
	Error	180	0.155		
D	Morph	1	0.004	0.048	0.82
	Sex	1	0.003	0.039	0.84
	Morph \times sex	1	0.071	0.873	0.35
	Error	325	0.082		

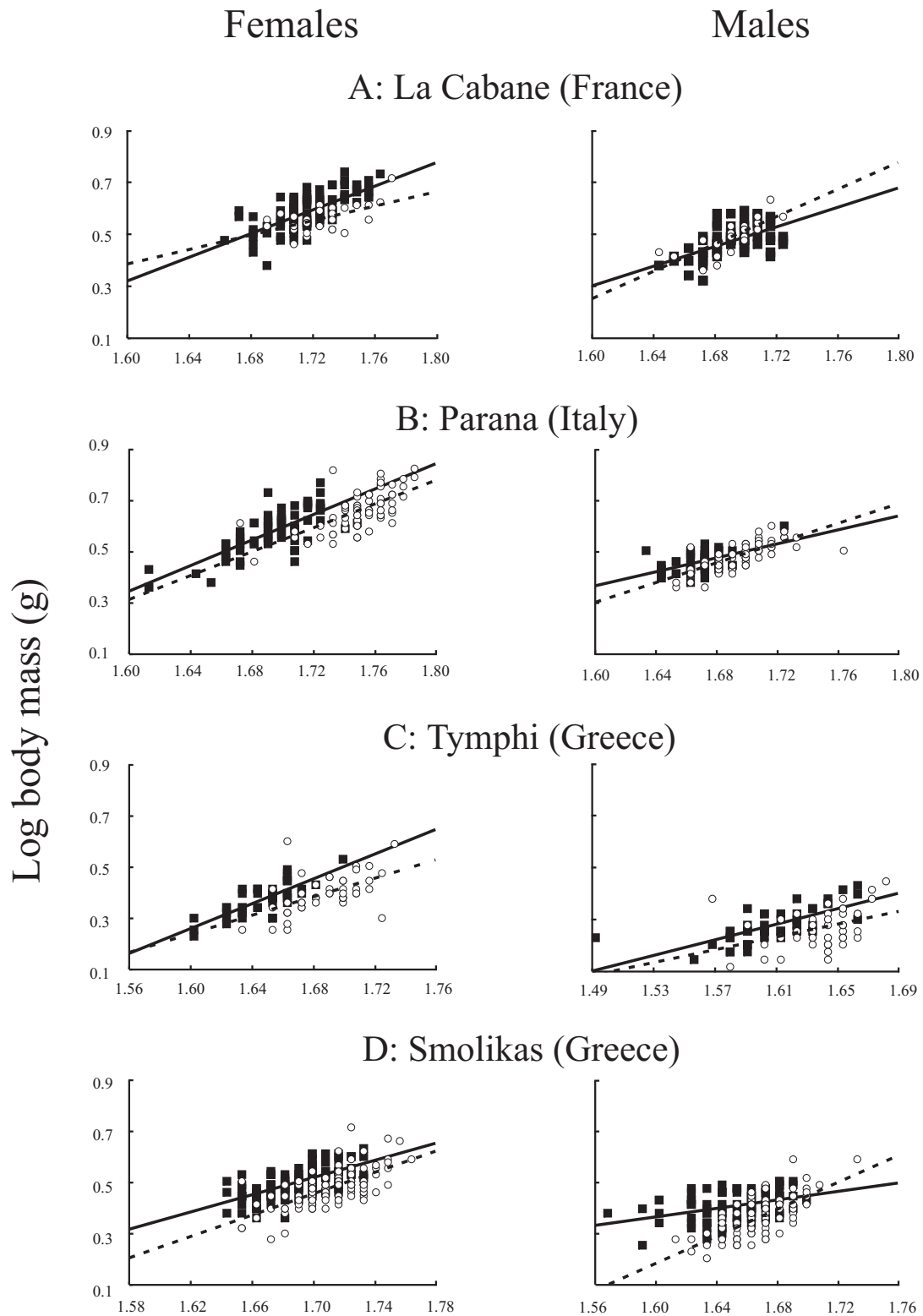


Figure 1. Linear regressions of $\log(\text{body mass, g})$ on $\log(\text{snout-vent length, mm})$ for Alpine newt pedomorphs (full squares and solid lines) and metamorphs (open circles and dashed lines) in four populations. See Table 2 for the significance of the differences between morphs.

tages taken by the newts engaged in a paedomorphic ontogenetic pathway. Laboratory experiments have also revealed higher capture success rates in pedomorphs than metamorphs for several aquatic prey types (Whiteman et al., 1996; Denoël, 2001).

Our results converge with the ‘paedomorph advantage hypothesis’ (Whiteman, 1994), as pedomorphs exhibited better body condition than metamorphs in most of the studied populations and better for-

aging efficiency in half of them. However, this agreement with the ‘paedomorph advantage hypothesis’ could mask disparities among populations in the proximal mechanisms that induce paedomorphosis (high vs. low larval growth rates). At site B (lowland pond), paedomorphic individuals grow faster than metamorphs (Denoël & Joly, 2000). They are thus more efficient than metamorphs in exploiting resources from the aquatic habitat and remain in this

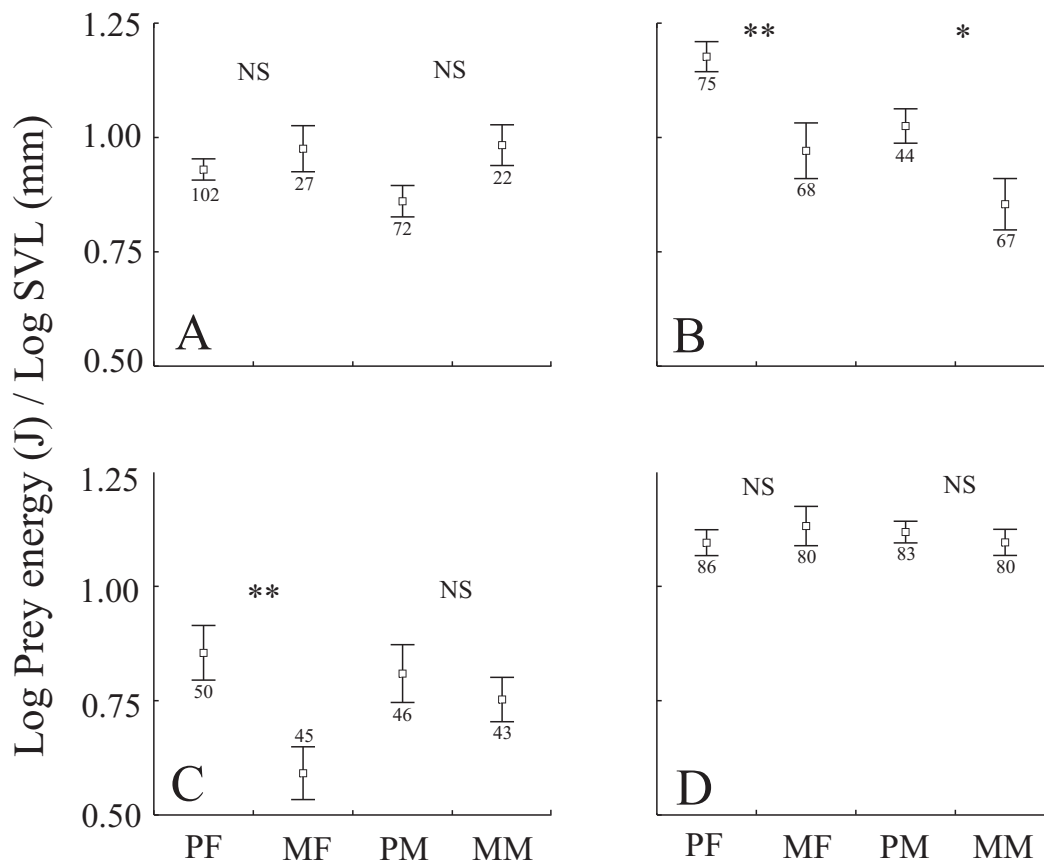


Figure 2. Mean (\pm SE) energy equivalent of stomach contents (log-transformed values weighted by snout-vent length, in Joules) in four populations of the Alpine newt. PF: paedomorphic females, MF: metamorphic females, PM: paedomorphic males, MM: metamorphic males, SVL: snout-vent length. NS, $P > 0.05$, * $P < 0.05$, ** $P < 0.01$ (post hoc LSD test between morphs within each sex; see Table 3 for anova statistics).

habitat while metamorphs leave water each year after the breeding season. Paedomorphs at site B also reach sexual maturity long before metamorphs, thus improving their reproductive lifetime fitness (Denoël & Joly, 2000). In contrast, the advantage of paedomorphic individuals at site A (high-elevation lake) mainly lies in better body condition as both overall growth and age at maturity are similar between morphs (Denoël & Joly, 2000). In such mountain lakes, one can thus expect that paedomorphosis is primarily promoted by low larval growth. The avoidance of the costs related to complex life cycles nevertheless allow paedomorphs to exhibit higher body conditions than adult metamorphs. As a consequence, larvae opting for paedomorphosis because of initial low growth rates may later draw some advantage from paedomorphosis (during both juvenile and adult stages), allowing them to counterbalance the initial size deficit.

Body size can also affect the success of individuals as this trait is correlated with fecundity in salamanders (Semlitsch, 1985). Paedomorphs were of similar size to metamorphs at one site, but were smaller than metamorphs at the others (Denoël & Joly, 2000; Denoël, 2001). Despite better body condition, fecundity may be hampered by lower body size in progenetic paedomorphs. However, in such organisms with indeterminate growth and high adult survival and fecundity (Joly & Grolet, 1996; Kalezić et al., 1996; Denoël & Joly, 2000), a slight decrease in the age at maturity may compensate for smaller adult body size (Kozłowski & Wiegert, 1986; Kozłowski & Uchmanski, 1987; Roff, 1992; Stearns, 1992). In the smooth newt, paedomorphic females produce more eggs than metamorphic ones (Kalezić et al., 1996; Rot-Nikčević, Kalezić & Džukić, 2000).

However, such a difference between morphs was not detected in the study of Alpine newt populations by Kalezić et al. (1996). Moreover the possibility for a paedomorphic newt to undergo metamorphosis at any age (Denoël & Poncin, 2001) may contribute to increase lifetime reproductive success. Differences between morphs might then be related to cost-benefit balances that are specific to the studied populations (Whiteman, 1994; Whiteman et al., 1996).

Because body condition did not vary accordingly in both sexes, the modalities of paedomorphosis may not necessarily be similar for each sex, as previously outlined in ambystomatid salamanders (Whiteman, 1997). High lipid storage may be more crucial for female fitness than for male fitness because of higher investment of females in gamete production (Pinder et al., 1992). Similar observations have been made in dispersal polymorphisms in insects (Roff, 1984; Roff & Fairbairn, 1993).

Higher storage of biological fuels probably contributes to the persistence of paedomorphosis as a valuable alternative tactic in urodele amphibians. By foregoing metamorphosis in harsh habitats, the newts take long-term advantages from the aquatic habitat and avoid the costs related to metamorphosis and habitat switching. This consideration of long-term advantages brings new elements to the theoretical conceptions of the ecology of amphibian metamorphosis (Wilbur & Collins, 1973; Whiteman, 1994). These results highlight the role of local contingencies (suitability of aquatic vs. terrestrial habitats) on the success of different ontogenetic pathways. Probably, each taxon involved in the differentiation of alternative ontogenetic pathways indeed deals with specific local ecological constraints. Our study shows the interest of considering cost-

benefit balance at different time scales to explain the maintenance of alternative phenotypes. Further studies that model population dynamics in integrating lifetime reproductive success should bring a new light on this evolutionary process.

Acknowledgements

We thank A. De Robertis, E. Pattee and two anonymous reviewers for helpful comments on the manuscript. Field work has benefited from the help of G. Hauseder and U. Schiffner; E. Kamtsiou, J.-M. Izoard, N. Kosias and J.-L. Prieur helped us in carrying the equipment to the lake; D. Vergos allowed us to stay in a log cabin close to the study sites; R. Clairin and M. Barbey (ONF), R. Leautaud (Mairie du Lauzet), and H. Savornin (Mairie de Montclar) permitted us to work at the lake in France; F. Andreone, M. Breuil, C. Giacomini, G.H. Parent and K. Sotiropoulos provided detailed information about the newt breeding sites. This research was authorized by the French and Greek ministries of the Environment, and supported by the Fonds pour la Formation à la Recherche dans l'Agriculture et dans l'Industrie, Fonds National de la Recherche Scientifique, Concours des Bourses de Voyage, Fondation Lefranc, Patrimoine de l'Université de Liège and Amadeus project. M. Denoël is Chargé de recherches du Fonds National de la Recherche Scientifique (Belgium).

References

- Barnes H, Blackstock J. 1973. Estimation of lipids in marine animals and tissues: detailed investigation of the sulphophovanillin method for 'total' lipids. *Journal of Experimental Biology and Ecology* 12: 103–118.
- Bizer JR. 1978. Growth rates and size at metamorphosis of high elevation populations of *Ambystoma tigrinum*. *Oecologia* 38: 175–184.
- Blackstone NW, Buss LW. 1993. Experimental heterochrony in hydractiniid hydroids: why mechanisms matter. *Journal of Evolutionary Biology* 6: 307–327.
- Bradshaw AD. 1985. Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* 13: 115–155.
- Cummins KW, Wuicheck JC. 1971. Caloric equivalents for investigations in ecological energetics. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 18: 1–158.
- Day RW, Quinn GBP. 1989. Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs* 59: 433–463.
- Denoël M. 2001. Avantages sélectifs d'un phénotype hétérochronique. *Eco-éthologie des populations pédomorphiques du triton alpestre, Triturus alpestris* (Amphibia, Caudata). Unpublished DPhil Thesis, University of Liège.
- Denoël M, Duguet R, Dzucic G, Kalezic M, Mazzotti S. 2001a. Biogeographical and ecological aspects of paedomorphosis in *Triturus alpestris* (Amphibia, Caudata). *Journal of Biogeography* 28: 1271–1280.
- Denoël M, Joly P. 2000. Neoteny and progenesis as two heterochronic processes involved in paedomorphosis in *Triturus alpestris* (Amphibia, Caudata). *Proceedings of the Royal Society London, Biological Sciences*, B 267: 1481–1485. Doi: 10.1098/Rspb.2000.1168.
- Denoël M, Joly P. 2001a. Adaptive significance of facultative paedomorphosis in *Triturus alpestris* (Amphibia, Caudata): resource partitioning in an alpine lake. *Freshwater Biology* 46: 1387–1396.
- Denoël M, Joly P. 2001b. Size-related predation reduces intramorph competition in paedomorphic Alpine newts. *Canadian Journal of Zoology* 79: 943–948.
- Denoël M, Poncin P. 2001. The effect of food on growth and metamorphosis of paedomorphs in *Triturus alpestris apuanus*. *Archiv für Hydrobiologie* 152: 661–670.
- Denoël M, Poncin P, Ruwet JC. 2001b. Sexual compatibility between two heterochronic morphs in the Alpine newt, *Triturus alpestris*. *Animal Behaviour* 61: 559–566. doi: 10.1006/anbe.2001.1793.
- Fasola M. 1993. Resource partitioning by three species of newts during their aquatic phase. *Ecography* 16: 73–81.
- Gould SJ. 1977. *Ontogeny and phylogeny*. Cambridge: Belknap press.
- Harris RN. 1987. Density-dependent paedomorphosis in the salamander *Notophthalmus viridescens dorsalis*. *Ecology* 68: 705–712.
- Hervant F, Mathieu J, Durand J. 2001. Behavioural, physiological and metabolic responses to long-term starvation and refeeding in a blind cave-dwelling (*Proteus anguinus*) and a surface-dwelling (*Euproctus asper*) salamander. *Journal of Experimental Biology* 204: 269–281.
- Jakob EM, Marshall SD, Uetz GW. 1996. Estimating fitness: a comparison of body condition indices. *Oikos* 77: 61–67.
- Jiang S, Claussen DL. 1992. A bioenergetic budget for overwintering newts (*Notophthalmus viridescens*) from southern Ohio: their fat reserves and aerobic metabolic rates in water. *Comparative Biochemistry and Physiology* 101A: 743–750.
- Joly P, Grolet O. 1996. Colonization dynamics of new ponds, and the age structure of colonizing Alpine newts, *Triturus alpestris*. *Acta Oecologica* 17: 599–608.
- Jorgensen SE. 1979. *Handbook of environmental and ecological parameters*. Oxford: Pergamon Press.
- Kalezic ML, Cvetkovic D, Djorovic A, Dzucic G. 1996. Alternative life-history pathways: paedomorphosis and adult fitness in European newts (*Triturus vulgaris* and *T. alpestris*). *Journal of Systematic Zoology and Evolutionary Research* 34: 1–7.
- Kozłowski J, Uchmanski J. 1987. Optimal individual growth and reproduction in perennial species with indeterminate growth. *Evolutionary Ecology* 1: 214–230.
- Kozłowski J, Wiegert RG. 1986. Optimal allocation of energy to growth and reproduction. *Theoretical Population Biology* 29: 16–37.
- Laurenti JN. 1768. *Specimen Medicum Exhibens Synopsin Reptilium*. Wien (1996 reprint: A. Asher, Amsterdam).
- Leclerc RF, Regier JC. 1990. Heterochrony in insect development and evolution. *Seminars in Developmental Biology* 1: 271–279.
- Livezey BC. 1992. Flightlessness in the Galapagos Cormorant (*Compsobalieu [Nannopterum] harrisi*): heterochrony, giantism, and specialization. *Zoological Journal of the Linnean Society* 105: 155–224.
- McKinney ML, McNamara KJ. 1991. *Heterochrony. The evolution of ontogeny*. New York: Plenum Press.
- McNamara KJ. 1983. The earliest *Tegulorhynchia* (Brachiopoda: Rhynchonellida) and its evolutionary significance. *Journal of Paleontology* 57: 461–473.
- Meyer A. 1987. Phenotypic plasticity and heterochrony in *Cichlasoma managuense* (Pisces, Cichlidae) and their implications for speciation in Cichlid fishes. *Evolution* 41: 1357–1369.
- Miaud C. 1990. La dynamique des populations subdivisées: étude comparative chez trois amphibiens urodèles (*Triturus alpestris*, *T. helveticus* et *T. cristatus*). Unpublished DPhil Thesis, Claude-Bernard University, Lyon.
- Pinder AW, Storey KB, Ultsch GR. 1992. Estivation and hibernation. In: Feder ME, Burggren WW, eds. *Environmental physiology of the amphibians*. Chicago: Chicago University Press. 250–274.
- Roff DA. 1984. The cost of being able to fly: a study of wing polymorphism in two species of crickets. *Oecologia* 63: 30–37.
- Roff DA. 1992. *The evolution of life histories*. New York: Chapman & Hall.
- Roff DA, Fairbairn DJ. 1993. The evolution of alternative morphologies: fitness and wing morphology in male sand crickets. *Evolution* 47: 1572–1584.
- Rot-Nikcevic I, Kalezic ML, Dzucic G. 2000. Paedogenesis, life history traits and sexual dimorphism: a case study of the smooth newt, *Triturus vulgaris*, from Pannonia. *Folia Zoologica* 49: 41–52.
- Ryan TJ, Semlitsch RD. 1998. Intraspecific heterochrony and life history evolution: decoupling somatic and sexual development in a facultatively paedomorphic salamander. *Proceedings of the National Academy of Sciences USA* 95: 5643–5648.
- Scheiner SM. 1993. Genetics and the evolution of phenotypic plasticity. *Annual Review in Ecology and Systematics* 24: 35–68.
- Schlichting CD. 1986. The evolution of phenotypic plasticity in plants. *Annual Review in Ecology and Systematics* 17: 667–693.
- Schlichting CD, Pigliucci M. 1998. Phenotypic evolution. A reaction norm perspective. Sunderland: Sinauer.
- Scott DE, Fore MR. 1995. The effect of food limitation on lipid levels, growth, and reproduction in the marbled salamander, *Ambystoma opacum*. *Herpetologica* 51: 462–471.

- Semlitsch RD. 1985. Reproductive strategy of a facultatively paedomorphic salamander *Ambystoma talpoideum*. *Oecologia* 65: 305–313.
- Semlitsch RD. 1987. Paedomorphosis in *Ambystoma talpoideum*: effects of density, food, and pond drying. *Ecology* 68: 994–1002.
- Semlitsch RD, Wilbur HM. 1989. Artificial selection for paedomorphosis in the salamander *Ambystoma talpoideum*. *Evolution* 43: 105–112.
- Shea BT. 1983. Paedomorphosis and neoteny in the pygmy chimpanzee. *Science* 222: 521–522.
- Sprules WG. 1974. Environmental factors and the incidence of neoteny in *Ambystoma gracile* (Baird) (Amphibia: Caudata). *Canadian Journal of Zoology* 52: 1545–1552.
- Stanley SM. 1972. Functional morphology and evolution of bysally attached bivalve molluscs. *Journal of Paleontology* 46: 165–212.
- Stearns SC. 1992. *The evolution of life histories*. Oxford: Oxford University Press.
- Werner EE. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *American Naturalist* 128: 319–341.
- Whiteman HH. 1994. Evolution of facultative paedomorphosis in salamanders. *Quarterly Review of Biology* 69: 205–221.
- Whiteman HH. 1997. Maintenance of polymorphism promoted by sex-specific fitness payoffs. *Evolution* 51: 2039–2044.
- Whiteman HH, Wissinger SA, Brown WS. 1996. Growth and foraging consequences of facultative paedomorphosis in the tiger salamander, *Ambystoma tigrinum nebulosum*. *Evolutionary Ecology* 10: 433–446.
- Wilbur HM, Collins JP. 1973. Ecological aspects of amphibian metamorphosis. *Science* 182: 1305–1314.
- Zar JH. 1996. *Biostatistical analysis*. London: Prentice Hall International.

Received 6 February 2002; accepted for publication 30 May 2002; Article first published online: 28 Aug 2002