Paedomorphosis in the Alpine newt (*Triturus alpestris*): decoupling behavioural and morphological change

Mathieu Denoël

Laboratory of Ethology and Animal Psychology, Department of Life Sciences, University of Liège, Quai Van Beneden 22, 4020 Liège, Belgium

Abstract

Paedomorphosis is a heterochronic pattern leading to morphological change, i.e. retention of larval characters in the adult phenotype. The aim of this study was to find out whether behaviour and morphology are decoupled in heterochronic phenotypes. To this end, I compared qualitative and quantitative aspects of courtship behaviour in syntopic metamorphic and paedomorphic Alpine newts, *Triturus alpestris*. Morphologically, the two morphs differ considerably (e.g. by the presence of gills only in paedomorphs), but their patterns of sexual behaviours are exhibited at similar frequencies and males use the same alternative reproductive tactics to attract unresponsive females. These results show that morphology and behaviour follow different ontogenetic pathways and are thus decoupled. Decoupling of the two traits offers the possibility of morphological evolution without alteration of sexual patterns.

Keywords. Heterochrony - Polymorphism - Courtship behaviour - Alternative mating tactics - Newts

Introduction

Paedomorphosis is a heterochronic process involving the retention of larval traits in the adult (Gould 1977). This developmental process has been inferred from paleontological data and is hypothesised to play an important role in species evolution (De Beer 1951; Gould 1977; McKinney and McNamara 1991).

Species with complex life-cycles are particularly predisposed to show radical heterochronic changes, because shifts in the timing of maturity can yield an adult phenotype radically different from that of the ancestor (McKinney and McNamara 1991; Cunningham and Buss 1993).

Although heterochronies usually concern morphology, they can also affect behaviour (McKinney and McNamara 1991; McKinney and Gittleman 1995; McNamara 1997). However, this area of research has been underexploited. Bird song is one of the rare known examples of a behavioural pattern that may show heterochrony (Irwin 1988). Morphological and behavioural heterochronies may also be coupled (Shea 1988) in animals such as chimpanzees (Shea 1983), canids (Price 1984; Wayne 1986) and palm-tangers (McDonald and Smith 1990, 1994). Selective breeding experiments have evidenced that heterochronic behavioural changes can occur quickly in populations of mice (Gariepy et al. 2001).

When morphological heterochrony arises within a species, it offers the possibility of comparing the behavioural patterns of syntopic individuals with a similar history. In newts and salamanders, facultative paedomorphosis is a common phenomenon. Some adults retain larval traits such as gills and gill slits whereas others are fully metamorphosed (Semlitsch and Wilbur 1989; Whiteman 1994). Paedomorphic phenotypes can be produced by different heterochronic processes involving different decouplings of sexual maturation and somatic development (Ryan and Semlitsch 1998; Denoël and Joly 2000). Both genetic and environmental factors affect individual developmental pathways (Harris 1987; Semlitsch 1987; Voss 1995; Denoël and Poncin 2001). Resource partitioning between morphs (Whiteman et al. 1996; Denoël and Joly 2001), earlier maturity in paedomorphs (Ryan and Semlitsch 1998; Denoël and Joly 2000), and a different breeding frequency in the two morphs (Whiteman 1997) are factors favouring dimorphism.

It is known that paedomorphs of at least some species can breed with both metamorphic and paedomorphic mates (Semlitsch and Wilbur 1989; Krenz and Sever 1995; Whiteman et al. 1999; Denoël et al. 2001a). In the Alpine newt, the two heterochronic morphs, although morphologically different, are sexually compatible, i.e. the success rates of homotypic and heterotypic crosses are equal, and mate choice by females does not seem biased toward paedomorphs or metamorphs (Denoël et al. 2001a).

Sexual behaviour of metamorphic newts and salamanders has been studied intensively in laboratory experiments since the end of the 1970s (reviewed, for example, in Verrell 1989; Halliday 1990; Denoël

1999), but no detailed data are available for paedomorphic individuals. Behavioural patterns of metamorphic Alpine newts have also been documented (Halliday 1977; Verrell 1988; Arntzen and Sparreboom 1989; Andreone 1990; Denoël 1996, 1998; Denoël et al. 2001a, b).

A sexual encounter in the Alpine newt typically starts with the orientation phase during which the male meets the female and pursues her if she moves away. The male then exhibits several caudal displays (display phases), deposits spermatophores on the substratum, and again exhibits several caudal displays (sperm transfer phase). The female can be responsive to the male (movement toward him) or unresponsive (remaining stationary or moving away from him).

The aim of this study was to determine whether behavioural and morphological changes can be decoupled in an ectothermic vertebrate, the Alpine newt. In other words, do morphologically paedomorphic and metamorphic males show the same sexual displays, produce them at similar frequencies, and use different alternative reproductive tactics, such as luring movements, to court females?

Methods

Adult Alpine newts (n=120) were caught by dipnetting in a French Alpine lake, Lac de la Cabane (44°24'N/6°24'E, 1,950 m elevation), in May 1998 (paedomorphs: 32 males and 36 females; metamorphs: 28 males and 24 females). The newts were caught the week after the lake thawed, i.e. at the start of the breeding season when most individuals have not yet been involved in sexual interactions. Paedomorphic individuals show open gill slits, unlike metamorphic individuals whose gill slits are closed. The two morphs have similar body size (paedomorphs: mean ± SE = 47.6 ± 0.4 mm, n=45; metamorphs: 47.0±0.4 mm, n=34; U=591.5, Z=1.718, P=0.8). The specimens were stored in refrigerated boxes from the time they were caught until they reached the laboratory. The different sexes and morphs were kept separately in seven aquaria (3 m^3 total water volume). The newts were toe-clipped to allow identification of individuals (Twitty 1966). This marking technique does not affect the survival or body condition of *Triturus* newts (Arntzen et al. 1999). The newts were fed four times a week with *Chironomus* larvae and *Daphnia*. The temperature ranged between 12.5 and 14.5°C and photoperiod was 14 h light /8 h dark. These laboratory conditions are within the range encountered by the newts in the field during the breeding season. All newts were released in their native habitat after completion of the experiments.

Homotypic (i.e. within morph) paired encounters (n=158) were staged in the 40 days after the capture date, i.e. within the normal breeding period of the species. Encounters involved 99 paedomorphic and 59 metamorphic crosses. All encounters were unique, as no individual male encountered the same female more than once. However, because some individuals were used more than once, some dependence between encounters remains. To alleviate this problem in the analyses, the values for each individual were averaged before computing statistical tests. An analysis of the success rates of these encounters has been presented in another paper (Denoël et al. 2001a). Because data did not fit a normal distribution, non-parametric tests were used to test for significant differences between morphs (Mann-Whitney U-test). To compare the frequencies of male behaviour patterns with unresponsive (remaining stationary or moving away from the male) and responsive (moving toward the male and/or picking up a spermatophore) females, a Wilcoxon paired-sample test was used. A chi-square test was computed to compare proportions of events in the morphs (movements to water surface). An absolute frequency is defined as the total number of a behavioural act that is exhibited by a male during one encounter. A relative frequency corresponds to the absolute number of a behavioural act divided by the total number of acts that are exhibited during the sperm-transfer phase of an encounter.

Experiments were conducted in an aquarium measuring 45x30x25 cm with the bottom covered with gravel. The water temperature was kept at mean ± SD = 14.0 ± 0.5 C, and the light intensity was 5,000 lux at the bottom of the aquarium. Behavioural patterns were recorded with a Sony Hi8 camcorder. If the male did not display during the first 45 min after the start of the experiment, both individuals were replaced with two new ones. Observations were conducted until the end of the sexual activities between the two partners. The tank water was replaced after each experiment. Videotapes were screened and male behavioural acts were encoded on a computer. Subsequent viewing of the tapes made it possible to note the behaviour of the female following each male act.

Results

Qualitative aspects of sexual behaviour

Courtship was similar in paedomorphs and metamorphs. It consisted of four phases, which have been previously described for metamorphs (see, for example, Denoël 1996; Denoël et al. 2001b), but not for paedomorphs. A summary is given below.

Orientation phase

The encounter starts with a mobile phase where the male meets the female, may touch her and follow her if she moves away.

Fanning display phase

The male, in a static posture in front of the female, may fold his tail against his flank and beat it rapidly. Fanning bouts are interrupted by pauses (static fan) or by slow undulation of the tail-tip (wiggle-tail-bent). While he is fanning, the male may also occasionally move his tail against his other flank (inversion).

Cat-buckle with lean-in display phase

The male may raise his body by extending his legs and arching his back, and move his tail toward the female (cat-buckle with lean-in). He also exhibits fanning bouts between these acts. The phase usually ends with a behaviour not yet described: the "rower". During the rower, the male, body close to the floor and tail partially folded against the flank, moves backwards and forwards without moving the point of contact of the feet with the floor.

Sperm-transfer phase

The male turns away and creeps ahead of the female (creep), moving or not his tail (quiver). He

Table 1. Mean absolute frequencies (±SE) of behavioural patterns exhibited by metamorphic (n=16) and paedomorphic (n=22) Alpine newt males

Phase	Behaviour	Metamorphs	Paedomorphs	U	Z	P
Display	Fan	80.5±12.9	69.7±10.3	154	0.650	0.52
	Static fan	64.8±11.0	55.4±9.4	152.5	0.695	0.48
	Wiggle-tail-bent	2.1±0.5	3.0±0.8	161.5	-0.429	0.67
	Inversion	1.5±0.4	2.9±0.6	124	-1.537	0.12
	Cat-buckle with lean-in	3.8±1.1	3.6±0.6	169	-0.207	0.84
	Rower	0.7±0.2	0.5±0.2	146.5	0.870	0.38
	Touch	0.9±0.5	0.2±0.1	148	0.828	0.41
Transfer	Creep	5.1±0.9	4.0±0.7	148	0.828	0.41
	Quiver	0.7±0.3	0.3±0.1	149	0.798	0.43
	Tail-fold	5.0±0.9	3.8±0.7	145	0.917	0.36
	Deposition	2.9±0.6	2.6±0.4	175.5	0.015	0.99
	Trembling tail	2.6±0.6	2.4±0.4	171.5	-0.133	0.89
	Distal lure	0.5±0.2	0.4±0.1	140.5	1.050	0.29
	Wiggle-tail-bent	2.0±0.5	1.7±0.3	175	-0.030	0.98
	Lateral-tail	6.1±1.4	5.1±0.8	167	0.270	0.79
	Push-back	2.8±1.0	2.1±0.4	174.5	-0.044	0.97

may then fold his tail (tail-fold), deposit a spermatophore on the substratum (deposition), and then immediately adopt a position perpendicular to the female in which he may exhibit several caudal displays. He may show a display more or less similar to the wiggle-tail-bent of the display phase and another slow movement of the tail-tip, but with the tail held perpendicular to the body (distal lure). He may also slowly move the tail, holding it parallel to the body but distant to it (trembling tail) or hold the tail against his flank, sometimes waving it (lateral tail). The male may also apply his tail against the female's snout and push her violently back, i.e. in the direction of the spermatophore (push-back).

Quantitative aspects of sexual behaviour

The absolute frequencies of the different sexual displays exhibited by metamorphic and paedomorphic males during a sexual encounter did not differ significantly (Table 1).

There was no significant difference between morphs in the number of spermatophores deposited per encounter including sperm transfer (metamorphs: mean ± SE = 3.7 ± 0.6, n=15; paedomorphs: 3.1±0.3, n=17; U=109.5, Z=0.684, P=0.5). Males of both morphs deposited 1-9 spermatophores per encounter.

There was no significant difference between morphs in the proportion of time spent by males in displays (metamorphs: mean ± SE = 75.5 ± 3.8%, n=16; paedomorphs: 77.5±3.7%, n=22; U=149.5, Z=-0.784, P=0.43), in the ratio of the duration of fanning bouts to the time spent in fan and static fan (metamorphs: mean ± SE = 59.7 ± 3.9%, n=16; paedomorphs: 56.8±2.8%, n=21; U=143, Z=0.766, P=0.44; only encounters with at least 10 behavioural acts were considered), or in the mean duration of fanning bouts (metamorphs: mean ± SE = 6.9 ± 0.6s, n=15; paedomorphs: 7.1±0.4 s, n=22; U=156.5, Z=-0.263, P=0.79; only encounters with at least 10 fanning bouts where considered). Figure 1 represents the distribution of the durations of fanning bouts in the two morphs (fanning bouts greater than 30 s are not included; they account for only 3% of observations). There was no significant difference between morphs in the frequency of trips to the surface to breathe (metamorphs: 35% of the encounter, n=17; paedomorphs: 30% of the encounters, n=30; X^2=0.14, P=0.70).

There was no significant difference between morphs in the proportion of sperm-transfer phases initiated without a positive response from the female (metamorphs: mean ± SE = 35.1 ± 7.9%, n=16; paedomorphs: 37.9±6.4%, n=21; U=153.5, Z=-0.444, P=0.66) or in the proportion of sperm-deposition events without female's tail touch (metamorphs: mean ± SE = 42.0 ± 10.3%, n=14; paedomorphs: 38.5±7.2%, n=21; U=156, Z=0.048, P=0.96).

For five of the six behavioural patterns of the sperm-transfer phase, male paedomorphs and metamorphs both exhibited different frequencies according to the response of the female (Table 2). When the females responded negatively to the males, the males exhibited significantly more often the following behavioural patterns: "quiver", "distal lure" and "wiggle-tail-bent". When the females responded positively to the males, they exhibited mainly the "lateral tail" and the "push-back". "Trembling tail" was used equally with responsive and unresponsive females (Table 2). Considered separately according to the responsiveness or unresponsiveness of the females, the male behavioural patterns exhibited by the two morphs during the sperm-transfer phase did not differ significantly (P>0.05 for all comparisons; U-test; Table 2).

Discussion

Paedomorphic and metamorphic newts show a radically different morphology. The main heterochronic difference is the retention of the larval structure of the trophic and respiratory apparatus. Paedomorphs retain a gill mode of respiration and

an aquatic mode of feeding due to the presence of gill slits (Semlitsch and Wilbur 1989; Lauder and Shaffer 1993). Epigamic characters also differ radically between morphs, with paedomorphs being fatter and having a higher tail, and metamorphs presenting more dots on the flanks and a larger cloaca (Denoël et al. 2001a). These characteristics means that secondary sexual traits are juvenilised in paedomorphs. Yet this study shows that the two morphologically heterochronic morphs of the Alpine newt display the same courtship patterns at similar frequencies. Morphologically, paedomorphic newts thus follow a paedomorphic ontogenetic pathway, but they develop the typical sexual behaviour of the ancestral metamorph. Morphology and sexual behaviour are thus decoupled in this species.

Such connections between behavioural and morphological developmental shifts have been studied very little. The literature focuses mainly on mammals and birds (McKinney and McNamara 1991; McKinney and Gittleman 1995). In bonobos, a paedomorphic reduction in morphological sexual dimorphism is associated with juvenile social traits, such as a higher male-female affinity, less sexual differentiation in social structures, and an immature kind of copulation. Nevertheless, although these traits are typical of juveniles, juveniles cannot mate. There is thus a clear dissociation of the development between the soma and germen lines, but the subadult sexual behavioural patterns are retained in the paedomorphic species (Shea 1983, 1984). However, such phylogenetic discussions are critical because common chimpanzees are not the direct ancestors of bonobos (Wrangham 1986; Shea 1989). In mice, selective breeding experiments have provided evidence for paedomorphosis in social behaviour: after only 13 generations, the mice lines selected for low aggression showed juvenilisation, i.e. they fought less and did so later in life (Gariepy et al. 2001).

Although few studies have examined the connection between sexual and morphological heterochrony, heterochronic morphs or species are well known to exhibit particular non-sexual behavioural patterns (McKinney and McNamara 1991). This is not very surprising as behaviour is expected to change with the modification of structures. For instance, the feeding apparatus of paedomorphic newts and salamanders is larval with the the presence of gill slits. Consequently, the feeding behaviour of the two morphs clearly differs. In paedomorphs, the water sucked in with the prey is expelled through the gill slits, resulting in a unidirectional water flow. In metamorphs, this water flow is bi-directional, since water is expelled by the mouth as gill slits are closed (Lauder and Shaffer 1993). Each morph also forages on different prey (Denoël and Joly 2001).

In salamanders, age appears not to affect the success of males in at least two plethodontid species (Houck and Francillon-Vieillot 1988; Verrell 1991), but it is not known how sexual courtship varies with age. Some paedomorphic populations of newts are progenetic (Denoël and Joly 2000), resulting in paedomorphs that are younger than metamorphs. It would be interesting to test whether behavioural and morphological traits are decoupled in these progenetic individuals.

Many animal species have more than one solution to acquire mates; they exhibit alternative reproductive tactics that maximise their fitness (Arnold 1976; Gross 1996). When a female is unresponsive to the sexual behaviour of a male, the male may change tactics, clasping the female in amplexus (Verrell 1982) or using luring behaviours (Wickler
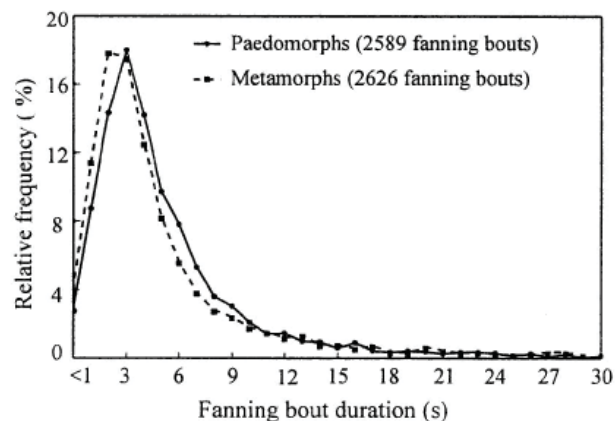

Fig. 1. Relative frequencies of fanning bout duration (s) in metamorphic and paedomorphic Alpine newt males

1968). Luring displays consist of slow movements of a part of the male body, such as the tip of the tail in metamorphic newts (Wambreuse and Bels 1984; Pecio and Rafinski 1985; Rafinski and Pecio 1992; Denoël et al. 2001b). In keeping with observations of Denoël et al. (2001b) on a Belgian population of metamorphic Alpine newts, the French metamorphic newts studied here used two luring movements with unresponsive females: the quiver, a slow undulation of the entire tail, and the distal lure, a slow movement of the tail tip positioned far from the body. They may also initiate the sperm-transfer phase and spermatophore deposition without any positive feedback from the female; this is a behavioural pattern well known in this species (Halliday 1990; Denoël et al. 2001b).

The use of alternative tactics can depend of the status of the individual, such as body size (Taborsky 1994; Gross 1996). The smallest individuals are usually those that sneak to fertilise females' eggs (Gross 1985; Poncin et al. 1996). Newts might also be expected to exhibit different alternative reproductive tactics according to their status - metamorph or paedomorph. However, that would be done independently of their body size because the size distributions are similar in the two morphs. Yet both metamorphs and paedomorphs use the two luring tactics to attract unresponsive females, and the frequencies of these behaviours, considered separately according to the responsiveness or unresponsiveness of the female, are similar in the two morphs.

The sexual activity of newts requires oxygen consumption. Males may thus have to leave the female to take air at the water surface. Such behaviour reduces the chance of again meeting the female upon returning to the bottom of the aquatic habitat (Halliday 1977). Because paedomorphs have a supplementary respiratory organ, the gills, they might be expected to leave the female less often than metamorphic males, which have no gills. This idea is reinforced by an observation of Seliskar and Pehani (1935), who found paedomorphs in an Alpine lake to take atmospheric air more rarely than metamorphs. However, from my own observations and those of Bovero et al. (1994, 1997), there is no difference between morphs for this trait. It is thus likely that gills of paedomorphs cannot meet the oxygen need during sexual activity. Nevertheless, the situation might be different in the deepest breeding places where the cost of moving to the surface might be larger.

Table 2. Mean relative frequencies (±SE, in %) of the behavioural patterns exhibited by metamorphic (n=13) and paedomorphic (n=17) Alpine newt males during sperm-transfer phase in front of unresponsive and responsive females (Wilcoxon paired-sample test)

Morph	Behaviour	Unresponsive females	Responsive females	Z	P
Metamorphs	Quiver	7.1±3.3	0	2.023	<0.05
	Distal lure	8.0±2.6	0	2.366	<0.05
	Wiggle-tail-bent	20.0±6.3	1.4±0.6	2.599	<0.01
	Trembling tail	19.6±7.3	12.5±3.3	0.524	0.60
	Lateral-tail	10.3±3.3	57.9±8.2	2.970	<0.01
	Push-back	1.9±2.1	18.2±4.0	2.520	<0.05
Paedomorphs	Quiver	9.9±3.3	0.1±0.1	2.366	<0.05
	Distal lure	7.5±2.7	0	2.366	<0.05
	Wiggle-tail-bent	33.1±5.6	6.0±3.1	2.947	<0.01
	Trembling tail	11.8±3.6	19.7±2.7	1.447	0.15
	Lateral-tail	15.8±4.0	53.8±4.7	3.051	<0.01
	Push-back	6.7±4.2	20.3±2.9	2.417	<0.05

The similarities of courtship behavioural patterns in the two heterochronic morphs of the Alpine newt may explain the observed sexual compatibility of the two morphs (Denoël et al. 2001a). Paedomorphic and metamorphic females show no selectivity against one of the two male morphs considering either sperm transfer or responsivity rates (Denoël et al. 2001a). Males of the two morphs display the typical behaviour of the species and are equally accepted by females during sexual interactions. These behavioural similarities allow frequent inter-morph breeding. These results show that morphology and behaviour follow different ontogenetic pathways and are thus decoupled. Decoupling of the two traits offers the possibility of morphological evolution without alteration of sexual patterns.

References

Andreone F (1990) Variabilita morfologica e riproduttiva in popolazioni di *Triturus alpestris* (Laurenti, 1768) (Amphibia, Urodela, Salamandridae). PhD Thesis, University of Bologna

Arnold SJ (1976) Sexual behavior, sexual interference and sexual defense in the salamanders *Ambystoma maculatum*, *Ambystoma tigrinum* and *Plethodon jordani*. Z Tierpsychol 42:247-300

Arntzen JW, Sparreboom M (1989) A phylogeny for the Old World newts, genus *Triturus*: biochemical and behavioural data. J Zool Lond 219:645-664

Arntzen JW, Smithson A, Oldham RS (1999) Marking and tissue sampling effects on body condition and survival in the newt *Triturus cristatus*. J Herpetol 33:567-576

Bovero S, Andreone F, Giacoma C (1994) Aspetti comportamentali in esemplari pedogenetici e metamorphosati di *Triturus alpestris apuanus*. Studi Trentini Sci Nat Acta Biol 71:151-155

Bovero, S, Giacoma C, Andreone F (1997) Sexual selection and facultative paedogenesis in the Alpine newt, *Triturus alpestris apuanus* (Bonaparte, 1839). Geobios Lyon 21:287-292

Cunningham CW, Buss LW (1993) Molecular evidence for multiple episodes of paedomorphosis in the family Hydractiniidae. Biochem Syst Ecol 21:57-69

De Beer GR (1951) Embryos and ancestors. Oxford University Press, London

Denoël M (1996) Etude comparée du comportement de cour de *Triturus alpestris alpestris* (Laurenti, 1768) et *Triturus alpestris cyreni* (Wolterstorff, 1932) (Amphibia, Caudata): approche évolutive. Cah Ethol 16:133-258

Denoël M (1998) The modulation of movement as a behavioral adaptation to extreme environments in the newt *Triturus alpestris cyreni*. J Herpetol 32:623-625

Denoël M (1999) Le comportement social des urodèles. Cah Ethol 19:221-258

Denoël M, Joly P (2000) Neoteny and progenesis as two heterochronic processes involved in paedomorphosis in *Triturus alpestris* (Amphibia, Caudata). Proc R Soc Lond B 287:1481-1485

Denoël M, Joly P (2001) Adaptive significance of facultative paedomorphosis in *Triturus alpestris* (Amphibia, Caudata): resource partitioning in an Alpine lake. Freshwater Biol 46:1387-1396

Denoël M, Poncin P (2001) The effect of food on growth and metamorphosis of paedomorphs in *Triturus alpestris apuanus*. Arch Hydrobiol 152:661-670

Denoël M, Poncin P, Ruwet JC (2001a) Sexual compatibility between two heterochronic morphs in *Triturus alpestris* (Caudata, Salamandridae). Anim Behav 62:559-566

Denoël M, Poncin P, Ruwet JC (2001b) Alternative mating tactics in the Alpine newt *Triturus a. alpestris*. J Herpetol 35:62-67

Gariépy JL, Bauer DJ, Cairns RB (2001) Selective breeding for differential aggression in mice provides evidence for heterochrony in social behaviours. Anim Behav 61:933-947

Gould SJ (1977) Ontogeny and phylogeny. Belknap Press, Cambridge, Mass

Gross MR (1985) Disruptive selection for alternative life histories in salmon. Nature 313:47-48

Gross MR (1996) Alternative reproductive strategies and tactics: diversity within sexes. Trends Ecol Evol 11:92-98

Halliday TR (1977) The courtship of European newts: an evolutionary perspective. In: Taylor DH, Guttman SI (eds) The reproductive biology of amphibians. Plenum Press, New York, pp 185-232

Halliday TR (1990) The evolution of courtship behavior in newts and salamanders. Adv Study Behav 19:137-169

Harris RN (1987) Density-dependent paedomorphosis in the salamander *Notophthalmus viridescens dorsalis*. Ecology 68:705-712

Houck LD, Francillon-Vieillot H (1988) Test for age and size effects on male mating success in a plethodontid salamander. Amphibia-Reptilia 9:135-144

Irwin RE (1988) The evolutionary importance of behavioural development: the ontogeny and phylogeny of bird song. Anim Behav 36:814-824

Krenz JD, Sever DM (1995) Mating and oviposition in paedomorphic *Ambystoma talpoideum* precedes the arrival of terrestrial males. Herpetologica 51:387-393

Lauder GV, Shaffer HB (1993) Design of feeding systems in aquatic vertebrates: major patterns and their evolutionary interpretations. In: Hanken J, Hall BK (eds) Functional and evolutionary mechanisms. University of Chicago Press, Chicago, pp 113-149

McDonald MA, Smith MH (1990) Speciation, heterochrony, and genetic variation in Hispaniolan palm-tanagers. Auk 17:707-717

McDonald MA, Smith MH (1994) Behavioral and morphological correlates of heterochrony in Hispaniolan palm-tanagers. Condor 96:433-446

McKinney ML, Gittleman JL (1995) Heterochrony in life history, morphology and behaviour. In: McNamara KJ (ed) Evolutionary change and heterochrony. Wiley, Chichester, pp 21-47

McKinney ML, McNamara KJ (1991) Heterochrony. The evolution of ontogeny. Plenum Press, New York

McNamara KJ (1997) Shapes of time. The evolution of growth and development. John Hopkins University Press, Baltimore, Md

Pecio A, Rafinski J (1985) Sexual behaviour of the Montandon's newt, *Triturus montandoni* (Boulenger) (Caudata: Salamandridae). Amphibia-Reptilia 6:11-22

Poncin P, Philippart JC, Ruwet JC (1996) Territorial and non-territorial spawning behaviour in the bream. J Fish Biol 49:622-626

Price EO (1984) Behavioral aspects of animal domestication. Q Rev Biol 59:1-32

Rafinski J, Pecio A (1992) The courtship behaviour of the Bosca's newt, *Triturus boscai* (Amphibia: Salamandridae). Folia Biol 40:155-165

Ryan TJ, Semlitsch RD (1998) Intraspecific heterochrony and life history evolution: decoupling somatic and sexual development in a facultatively paedomorphic salamander. Proc Natl Acad Sci USA 95:5643-5648

Seliskar A, Pehani H (1935) Limnologische Beiträge zum Problem der Amphibienneotenie. Verh Int Verein Theor Angew Limnol 7:263-294

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

Shea BT (1984) An allometric perspective on the morphological and evolutionary relationships between pygmy (Pan paniscus) and common (*Pan troglodytes*) chimpanzees. In: Susman R (ed) The pygmy chimpanzee: evolutionary biology and behavior. Plenum Press, New York, pp 89-130

Shea BT (1988) Heterochrony in primates. In: Mckinney ML (ed) Heterochrony and evolution. Plenum Press, pp 237-266

Shea BT (1989) Heterochrony in human evolution: the case for neoteny reconsidered. Yearb Phys Anthropol 32:69-10

Taborsky M (1994) Sneakers, satellites, and helpers: parasitic and cooperative behavior in fish reproduction. Adv Study Behav 23:1-100

Twitty VC (1966) Of scientists and salamanders. Freeman, San Francisco, Calif

Verrell PA (1982) The sexual behaviour of the red-spotted newt, *Notophthalmus viridescens* (Amphibia: Urodela: Salamandridae). Anim Behav 30:1224-1236

Verrell PA (1988) Sexual interference in the Alpine newt, *Triturus alpestris* (Amphibia, Urodela, Salamandridae). Zool Sci 5:159-164

Verrell PA (1989) The sexual strategies of natural populations of newts and salamanders. Herpetologica 45:65-282

Verrell PA (1991) Male mating success in the mountain dusky salamander, *Desmognathus ochrophaeus*: are small, young, inexperienced males at disadvantage? Ethology 88:277-286

Voss SR (1995) Genetic basis of paedomorphosis in the axolotl, *Ambystoma mexicanum*: a test of the single-gene hypothesis. J Hered 86:441-447

Wambreuse P, Bels V (1984) Analyse qualitative et quantitative de la parade sexuelle du triton palmé *Triturus helveticus* (Razoumowsky 1798). Cah Ethol Appl 4:193-218

Wayne RK (1986) Cranial morphology of domestic and wild canids: the influence of development on morphological change. Evolution 40:243-261

Whiteman HH (1994) Evolution of facultative paedomorphosis in salamanders. Q Rev Biol 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*. Evol Ecol 10:433-446

Whiteman HH, Gutrich JJ, Moorman RS (1999) Courtship behavior in a polymorphic population of the tiger salamander, *Ambystoma tigrinum nebulosum*. J Herpetol 33:348-351

Wickler W (1968) Le mimétisme animal et végétal. Hachette, Paris

Wrangham RW (1986) Ecology and social relationships in two species of chimpanzee. In: Rubenstein DI, Wrangham RW (eds) Ecological aspects of social evolution: birds and mammals. Princeton University Press, Princeton, pp 352-378

Contact Information:

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

Fax: +32-4-3665010