

Variations in age, size at maturity and gestation duration among two neighbouring populations of the alpine salamander (*Salamandra lanzai*)

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(Accepted 28 July 2000)

Abstract

We describe the age structures of two neighbouring terrestrial salamander populations. The skeletochronological method was also used on larvae *in utero* and on new-born individuals. The age of adults was 8–24 years in population A, while males reached maturity at 3–5 years old and the youngest females were 6 years old in population B. Males and females from population B were also larger than those in population A. For the first time, lines of arrested growth (LAGs) were also found in the humerus of intra-uterine larvae and new-born individuals, indicating that young can spend up to 3 years *in utero* (population B) and up to 4 years (population A) before hatching. Growth of adults (fitted by the Bertalanffy model) also exhibited differences in growth coefficient (k) and mean asymptotic length (SVL_{max}) between sexes and populations. Local climatic conditions differed between the two areas of these populations and we hypothesize that the number of rainy days directly influences foraging during the short period of activity (< 3 months), leading to a delay in age at maturity, smaller length and growth rate, and increased gestation duration in the drier environment. The discussion is focused on proximate environmental influences on the variation of length and associated life-history traits in ectotherms, especially in terrestrial salamanders.

Key words: phenotypic plasticity, age, size, gestation, skeletochronology, proximate cause

INTRODUCTION

Within a species range, several factors (i.e. climatic conditions, trophic resources, metabolic properties, interspecific competition and predator–prey interactions) may explain differences in body length and age. Since these causes are not mutually exclusive, it is difficult to determine their individual influence on the optimal size for species or the optimal size for a particular location (Kozłowski, 1992). This has been stressed also by the recent controversy over body length as a function of temperature, i.e. Bergmann's rule (Mousseau, 1997). The typical S-shaped growth curve (in which maturation is followed by a decreased or arrested rate of growth) exhibits a wide range of relationships between growth and age (reviews by Roff, 1992; Stearns, 1992). Numerous studies have examined proximate environmental influences on the expression of ectotherm life-history traits, and how such organisms respond when they are forced to grow slowly is one of

the basic questions of life-history theory (Stearns & Koella, 1986). In amphibians, variation in adult body size with respect to geographic gradients is reported in both anurans and urodeles: the frogs *Rana sylvatica* and *R. temporaria* increase in body size, age at maturity and longevity with altitude (Berven, 1982; Miaud, Guyétant & Elmberg, 1999), and with latitude in *R. septentrionalis* (Leclair & Laurin, 1996). The salamander *Desmognathus ocoee* and the newts *Triturus alpestris* and *T. marmoratus* mature at higher age and larger size in highland than in lowland populations (Tilley, 1980; Miaud, Guyétant & Faber, 2000). Such differences are also observed in neighbouring populations within the same region (Reading, 1988; Bruce & Hairston, 1990; Augert & Joly, 1993). Local trophic conditions have been proposed as a source of proximate variation in lizard (Ballinger, 1977; Dunham, 1978), frog (Augert & Joly, 1993) and salamander (Fraser, 1976) growth rates.

The aim of this paper is to compare the age, length and growth of individuals from two neighbouring populations of the alpine salamander *Salamandra lanzai*. This is a viviparous species endemic to a small area in south-west (Cottina) Alps (Nascetti *et al.*, 1988;

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Table 1. Climatological variables recorded at the Abriès and Crissolo meteorological stations, on the west and east slope of the Mount Viso massif, respectively. Data are average values from a 16-year (Abriès) and 10-year (Crissolo) chronicle

Location	Abriès (1560 m a.s.l.)					Crissolo (1410 m a.s.l.)				
	June	July	Aug	Sept	Total	June	July	Aug	Sept	Total
Cumulative rain (mm)	75.5	43.3	57.0	86.2	262	114.9	62.6	76.3	107.0	360.8
No. of rainy days	8.4	6.7	7.0	7.3	29.4	9.8	8.9	9.5	8.4	36.6
Average temperature (°C)	15.3	16.2	15.8	11.9	–	14.3	16.6	15.7	12.4	–

Grossenbacher, 1994), where it occurs between *c.* 1300 and 2800 m a.s.l. (Andreone & Sindaco, 1989; Ribéron, Miaud & Guyétant, 1996). The two populations studied inhabit the opposite slopes of the same mountains at similar altitude, but with contrasting rain conditions. Sexual maturation is a critical transition in the life history of any organism, as the age and size at maturity at which it occurs greatly influence fitness (Charlesworth, 1980; Bernardo, 1993; Adolph & Porter, 1996) and we compare age and size at maturity between the two populations. Age was determined by skeletochronology, the most reliable method of age estimation in amphibians (Halliday & Verrell, 1988; Castanet & Smirina, 1990), and the use of phalanges avoided sacrificing individuals. Moreover, this method was used on intra-uterine larvae to determine gestation duration. These results will be useful both for evaluating other field data and for constructing models of life-history evolution that incorporate proximate effects (Shine & Charnov, 1992; Adolph & Porter, 1996; Tracy, 1999).

MATERIAL AND METHODS

Study site, climatic variables and sampling

Both populations inhabit the slopes of the Mount Viso massif, in the south-west Alps, at the border of France and Italy. The western population (44°42'N, 7°03'W) is situated along a small tributary of the Guil River, at an altitude of 2170–2250 m a.s.l. The sampling zone was *c.* 160 × 80 m, consisting of typical alpine grassland with patches of dwarf juniper *Juniperus nana* and rhododendron *Rhododendron ferrugineum*, several blocks, crevices and rodent burrows providing salamander refuges (Ribéron *et al.*, 1996). The station has a mean slope of 30% and is oriented south–east.

The eastern population (44°40'N, 7°05'W) is situated in the upper Po valley on the eastern slope of the Mount Viso massif. The altitude is *c.* 2020–2070 m a.s.l. and the sampling zone measures *c.* 100 × 100 m. The area is crossed by several small streams and is partly occupied by an alpine moor (Andreone, 1992; Andreone, Giacomina *et al.*, 1996). The rest of the surface is covered by stones that together with complex crevices and other refuges provide hiding places for salamanders. The vegetation is typical alpine grassland.

Cumulative rainfall (mm), number of rainy days and average temperature refer to Abriès (1560 m, *c.* 7 km

from the western population) and Crissolo (1410 m, *c.* 6 km from the eastern population) meteorological stations (Table 1). The Mount Viso massif has an intra-alpine climate. The pluviometric gradient is more sensitive on the horizontal (east–west) axis than on the vertical one (Pache, Aime & Michalet, 1996). The pluviometric regime depends, at the scale of the massif, of a specific airflow called 'lombarde'. This wind, coming from east-south-east, fills with water over the Mediterranean Sea and causes high precipitation on the eastern slope of the Mount Viso massif. As a result, the western slopes of Mount Viso are characterized by a drier climate.

Salamanders were caught by hand during their active period (from mid-June to the end of August, 1994), during the night or on rainy days. Each individual was sexed by direct observation of the shape of the vent, their snout–vent length (SVL) measured to the nearest 1 mm with a plastic ruler and weighed to the nearest 0.1 g with an electronic balance. The longest digit (third or fourth) of the hind leg was removed and stored in 70% alcohol for skeletochronological analysis. Each individual was immediately released at the point of capture. Adults refer to mature individuals, *i.e.* those exhibiting external sexual characters (size and shape of vent). Juveniles refer to individuals without evident external sexual characters. New-borns were individuals with signs of recent birth, such as visible gill scars and a laterally compressed tail.

Skeletochronological analysis

Skeletochronology was applied to phalanges of adults and juveniles (western population 120 adults and 15 juveniles; eastern population, 197 adults and 6 juveniles). Thin sections (*c.* 14 or 16 µm thick) at the mid-shaft diaphysis of the decalcified phalanges were made with a freezing microtome and stained with Ehrlich's haematoxylin. The analysis of growth marks was made by 2 different persons, who had similar experience in the technique and who agreed on the identification criteria for lines of arrested growth (LAGs) and the final age estimation. For each individual, 1 bone section was photographed or drawn at the same magnification using a camera lucida. This allows simultaneous comparisons and facilitates the analysis of the pattern of bone growth marks. For intra-uterine larvae and new-borns (western population 6 larvae *in utero*; eastern population 8 larvae

in utero and 6 new-born individuals), femurs were used because of the small size of phalanges. Bones were embedded in epoxy resin, and prepared as (semi)-thin sections (1 μm thick) using an ultramicrotome and stained with toluidine blue.

Growth model and statistical analysis

Sexual size dimorphism (SSD) was calculated only on body length. We used the Lovich & Gibbons (1992) sexual dimorphism index (SDI) based on the simple ratio of SVL of the larger sex divided by SVL of the smaller sex, with the result arbitrarily defined as positive when females are larger than males.

Growth was estimated according to Bertalanffy's (1938) model: $\text{SVL}_t = \text{SVL}_{\text{max}} (1 - \exp^{-k(t-t_0)})$. Knowledge of size and age at birth allowed application of this model to amphibians (e.g. Hemelaar, 1988; Arntzen, 2000), i.e. $\text{SVL}_t = \text{SVL}_{\text{max}} - (\text{SVL}_{\text{max}} - \text{SVL}_{\text{birth}}) \exp^{-k(t-t_{\text{birth}})}$ where t is expressed as the number of growing seasons experienced (i.e. age). SVL_t represented the snout-vent length at age t . SVL_{max} is the estimated average maximum SVL that can be reached. $\text{SVL}_{\text{birth}}$ is the fixed average length at birth (i.e. 33.6 mm), and was estimated by the mean of the smallest immatures caught in both populations and SVL of pre-hatching juveniles of pregnant females. The corresponding t_{birth} , intercept on the time axis, was fixed at 0. The growth coefficient k , the rate at which SVL_{max} is approached, defines the shape of the curve. The parameters SVL_{max} and k and their asymptotic confidence intervals (CI) were estimated by non-linear least-square regression (Statistica 5.0/W, Statsoft Inc., U.S.A.). Two SVL_{max} and k were considered to be significantly different (at 0.95 level) when their confidence intervals did not overlap (Geller, 1983; El Mounden, Znari & Brown, 1999).

Parameters (age, length and mass) were compared with a t -test or Mann-Whitney U -test according to the normality of the data. Spearman correlation (r_s) coefficients were calculated between age and SVL. Small size of the juvenile sample in the eastern population ($n=6$) did not allow statistical comparisons.

RESULTS

Bone histology and bone growth dynamics at the femoral and phalanges midshaft diaphysis

As has been previously described (Fachbach, 1988) for *Salamandra atra*, at the end of embryonic life, i.e. the intra-uterine period, the cortex of the femoral midshaft diaphysis is a crown of embryonic woven fibred bone deposited on the primary cartilaginous core. In phalanges, this crown is thin. At hatching, just after metamorphosis in this direct developing species, the femoral marrow cavity seems to be already enlarged by endosteal resorption. At the same time, endosteal bone, separated by a reversal cementing line, begins to be

deposited inside the periosteal crown. After a small delay, periosteal parallel fibred bone is deposited around the embryonic bone. In the femur, part of this bone may be conserved in juveniles and adults (Fachbach, 1988). In phalanges, at the diaphysis level, some cartilage may remain in the marrow cavity until 4–5 years post-hatching (cartilage remains later at the metaphyseal levels). In older individuals, endosteal resorption can partly destroy the embryonic bone, before endosteal bone deposition.

Lines of arrested growth (LAG) were clearly visible and we assumed that, as in previous similar studies, counting the number of LAGs in cross-section of bones reveals the number of winters experienced by each individual.

Growth marks in intra-uterine larvae

One original result of this study is that LAGs are observed not only in the bone deposited after hatching, but also in the bone deposited before, i.e. during intra-uterine life, in the crown of woven embryonic bone tissue. Nevertheless, during the first year *in utero*, skeletal elements are mostly cartilaginous, and the arrest of osteogenesis during the first winter cannot be recorded (Fig. 1a). For the populations studied, one LAG appears in the inner part of the embryonic crown of the femur, close to the marrow cavity (Fig. 1b), in immatures caught in summer just before or after hatching. It corresponds to the LAG of the second intra-uterine winter. In some individuals with an enlarged marrow cavity, there is no LAG, but in others, especially new-borns, one additional LAG is present close to the periphery of the crown, and would obviously correspond to the third winter spent *in utero* (Fig. 1c). This suggests that these individuals can spend up to 3 years *in utero* before hatching. In some individuals, only in the western population, three embryonic LAGs are present. Thus, they would have spent up to 4 years *in utero*, 1 year more than the oldest larvae of the eastern population.

Growth marks in juveniles and adults

Because of the small thickness of the embryonic crown in phalanges, pre-hatching LAGs are more difficult to identify in this bone. However, in some new-born individuals one LAG (western population) or two LAGs (eastern population) can be observed in embryonic bone. For older individuals, especially after 5 or 6 years, this embryonic bone and the LAGs inside it disappear because of endosteal resorption. Even the first LAG deposited after hatching can be removed locally, but never completely disappears (Fig. 1d, e). This explains why we do not take into account the LAGs observed in embryonic bone for age estimation; for all juveniles and adults, the age is estimated yearly starting from hatching.

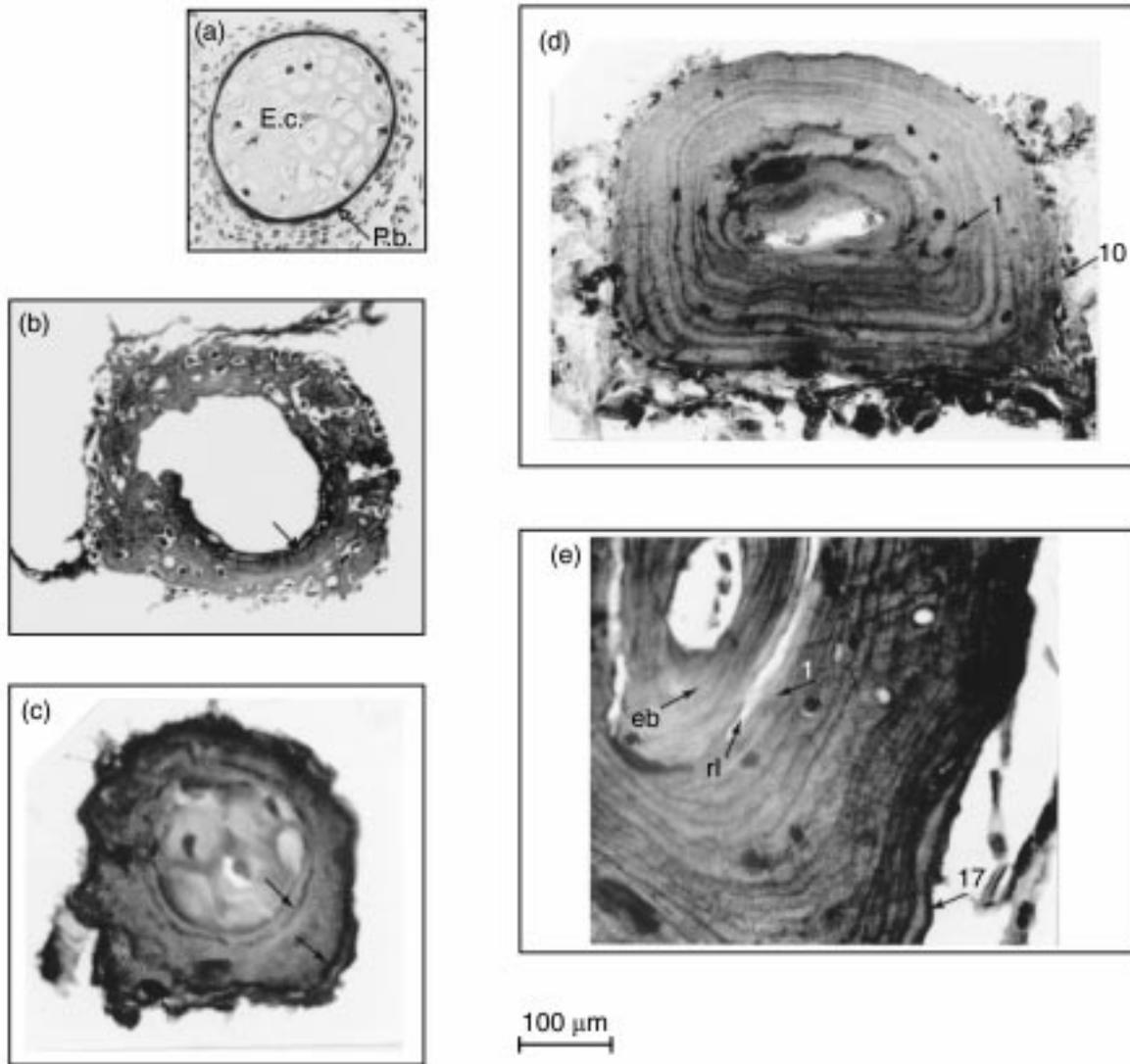


Fig. 1. Bone cross-sections for age determination in intra-uterine larvae, new-borns and adults of the alpine salamander *Salamandra lanzai*. (a) Larvae of close to the end of the first year spent *in utero* (Mount Viso, eastern population): 15.6 mm snout–vent length, cross-section (1 µm thick, toluidine blue) of the midshaft femoral diaphysis. At this age, the embryonic cartilage of the femur has just begun to be surrounded by a thin crown of periosteal bone. No lines of arrested growth (LAG) are observed. E.c., Embryonic cartilage; P.b., periosteal bone. (b) Intra-uterine larvae (Mount Viso, eastern population) taken just before hatching: 27.8 mm snout–vent length, cross-section (15 µm thick, Ehrlich’s haematoxylin) of the midshaft femoral diaphysis. The LAG of the second winter can be seen close to the narrow cavity (arrow). This larva has spent 2 years (2 winters) *in utero* before hatching. (c) New-born (Mount Viso, western population): cross section of the midshaft femoral diaphysis (15 µm thick) stained by Ehrlich’s haematoxylin. Two LAGs can be seen: the inner one, from the second winter, is close to the marrow cavity (arrow 1); the outer, from the third winter, is close to the periphery (arrow 2). Embryonic cartilage is still present in the marrow cavity. (d) Adult (Mount Viso, eastern population): cross-section (15 µm thick, Ehrlich’s haematoxylin) at the diaphysis level of a phalange. Ten LAGs. This individual collected in summer is 10 years old from hatching. (e) Adult (Mount Viso, western population): cross-section (15 µm thick, Ehrlich’s haematoxylin) at the diaphysis level of a phalange. Sixteen LAGs. This individual collected in summer is 16 years old from hatching. Note that LAGs are also present in the endosteal bone. e.b., endosteal bone; r.l., resorption line.

Age, length and mass between sexes in the western population

Descriptive statistics on age, body length and mass are reported in Table 2. Age of adults from the western population (Fig. 2a) did not differ significantly between

the sexes (Mann–Whitney *U*-test, $U = 961$, $P > 0.05$, d.f. = 94). LAGs were distributed from 8 to 23 years in males and 8–24 in females. Minimum age at maturity, i.e. age of the youngest individuals that exhibited external sexual characters, was 8 years in both sexes. Body length of adults did not differ significantly

Table 2. Descriptive statistics on age (years), body length (mm) and mass (g) of the alpine salamander *Salamandra lanzai* from two neighbouring populations (western and eastern populations) in the Cottian Alps. SVL, snout–vent length (mm); *n*, number; range: minimum and maximum values; sd, standard deviation; (χ^2 , chi-square result of normality test; d.f., degrees of freedom; *P*, probability)

	Western population							Eastern population						
	<i>n</i>	Mean	Range	SD	χ^2	d.f.	<i>P</i>	<i>n</i>	Mean	Range	SD	χ^2	d.f.	<i>P</i>
Males														
Age	61	14.4	8.0–23.0	3.21	6.24	4	0.180	74	11.2	3.0–22.0	4.01	4.64	4	0.330
SVL	61	80.2	70.0–93.0	4.48	5.50	5	0.360	74	82.8	64.4–94.5	5.44	5.45	6	0.490
Mass	61	11.6	8.5–15.5	1.62	7.81	5	0.160	74	11.1	5.0–16.4	2.33	2.04	5	0.840
Females														
Age	33	14.3	8.0–24.0	3.17	6.18	1	0.013	87	11.0	6.0–22.0	3.58	12.24	7	0.093
SVL	33	80.9	66.0–91.0	4.61	11.54	2	0.003	87	84.4	67.7–99.5	7.28	10.21	7	0.180
Mass	33	12.9	8.0–20.0	2.38	6.75	1	0.009	87	13.2	6.0–22.5	3.93	28.26	9	<0.001
Juveniles														
Age	15	2.6	1.0–5.0	1.35	–	–	–	4	–	3–5	–	–	–	–
SVL	15	51.8	34.0–67.0	9.68	–	–	–	6	58.1	41.6–69.4	9.21	–	–	–
Mass	15	4.5	1.5–7.5	2.0	–	–	–	6	5.1	2.0	1.92	–	–	–

between sexes (Mann–Whitney *U*-test, $U=902$, $P>0.05$, d.f. = 92). Minimum snout–vent length observed in mature adults was 70.0 mm in males and 66.0 mm in females (Table 2). The SDI was 0.0087. Females were significantly heavier than males (Mann–Whitney *U*-test, $U=625$, $P<0.05$, d.f. = 92). Part of this mass difference can be explained by gestation in females. Ages of juveniles ranged from 1 to 5 years. Age and SVL were highly correlated in juveniles ($r_s=0.90$, $t=9.79$, $P<0.0001$, $n=15$).

Age, length and mass between sexes in the eastern population

Mean age of adults from the eastern population (Fig. 2b) did not differ significantly between the sexes (*t*-test, $t=0.24$, $P>0.05$, d.f. = 159). LAGs were distributed from six to 22 in females and three to 22 in males. However, five males reached maturity at an age of 3–5 years while the youngest mature females had six LAGs. Body length of adults did not differ significantly (*t*-test, $t=-1.58$, $P>0.05$, d.f. = 159). Minimum SVL in mature adults was 64.4 and 67.7 mm in males and females, respectively (Table 2). The SDI was 0.019 in this population. Females were significantly heavier than males (Mann–Whitney *U*-test, $U=2238$, $P<0.001$, d.f. = 159). Age of juveniles ($n=6$) ranged from 1–5 years.

Comparisons of age, length and mass between populations

Males of the eastern population were younger (Mann–Whitney *U*-test, $U=1143$, $P<0.0001$, d.f. = 133) and larger (Mann–Whitney *U*-test, $U=0.0015$, $P<0.001$, d.f. = 133) than males of the western population, while mass did not differ significantly (Mann–Whitney *U*-test, $U=1962$, $P>0.05$, d.f. = 133) between these two populations.

As in males, females of the eastern population were younger (*t*-test, $t=4.54$, $P<0.0001$, d.f. = 118) and larger (*t*-test, $t=-2.56$, $P<0.05$, d.f. = 118) than females of the western population. Mass of females was also similar between these two populations (*t*-test, $t=-0.37$, $P>0.05$, d.f. = 118).

Sample size did not allow juvenile interpopulational comparisons (1- and 2-year-old juveniles were not caught in the eastern population). In the western population, the higher juvenile age (5 years) did not overlap with the smallest adult age (8 years), while in the eastern population the range of juvenile age overlapped with that of males only.

Characteristics of growth in the two populations

Growth was not estimated from recaptures of individuals: each point in the age/SVL relationship (Fig. 3) represented one individual, and the fitted growth model is thus a mean growth of the population. The growth coefficients (*k*) of males were significantly higher than those of females in both populations (Fig. 3, Table 3). On the other hand, the asymptotic sizes (SVL_{max}) of males were significantly lower than those of females in both populations.

Between populations, males of the eastern population grew faster than males of the western population (this difference was not significant for females). Female SVL_{max} in the eastern population was significantly higher than those in the western population but this difference was not significant for males.

DISCUSSION

Skeletochronological analysis

For *c.* 20 years, skeletochronology has been used in the

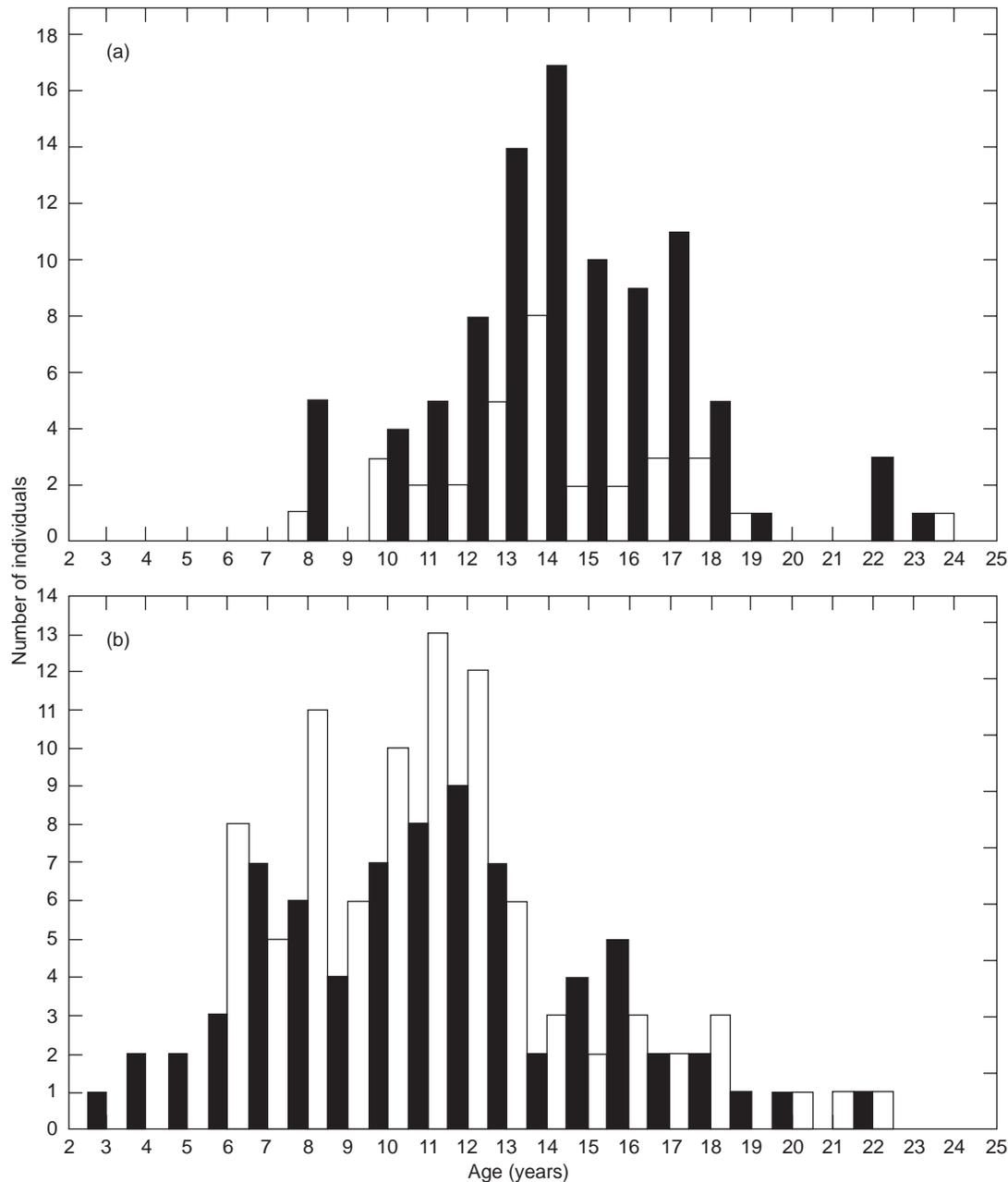


Fig. 2. Age distributions of adult alpine salamanders *Salamandra lanzai* from two neighbouring populations in the Cottian Alps: (a) western; (b) eastern. Open bars, males; black bars, females.

study of the population biology of tailed amphibians, e.g. Salamandridae (Smirina & Rocek, 1976; Hagström, 1977; Dolmen, 1982; Smirina & Sofianidu, 1985; Verrell & Francillon, 1986; Francillon-Vieillot, Arntzen & Géraudie, 1990; Forester & Lykens, 1991; Miaud, Joly & Castanet, 1993; Kuzmin, Dasgupta & Smirina, 1994; Andreone, De Michelis *et al.*, 1996; Diaz-Paniagua, Mateo & Andreu, 1996), Plethodontidae (Houck & Francillon-Vieillot, 1988; Wake & Castanet, 1995; Castanet, Francillon-Vieillot & Bruce, 1996; Parham, Dodd & Zug, 1996), and Ambystomatidae (Flageole & Leclair, 1992; Russell, Powell & Hall, 1996). The use of phalanges has allowed the estimation of individual age and growth without killing animals from wild popula-

tions. Counting LAGs in phalanges of *S. lanzai* was relatively easy, because of the clear arrest of growth during winter and the low degree of endosteal resorption. Analysis of the bones from intra-uterine larvae revealed that LAGs were also recorded in these larvae, and allowed an estimation of gestation duration of up to 3 years in the eastern population and up to 4 years in the western population. The small size of the samples used in this analysis cannot provide information about the variability of this time in either population, which therefore warrants a more detailed study. In populations of *S. atra* in the Alps, ranging from 600 to 1700 m a.s.l., gestation duration varied from 2 to 3 years depending on altitude (Guxé & Greven, 1994).

Table 3. Summary of growth parameters for two neighbouring populations (western and eastern) of the alpine salamander *Salamandra lanzai* in the Cottian Alps following the Von Bertalanffy model according to these viviparous salamander life cycle. n , number of individuals (where 13 and 5 juveniles were included in the western and eastern samples, respectively); k , growth coefficient; SVL_{max} , asymptotic SVL (mm); asymptotic 95% confidence intervals in parentheses; VR, variance explained in %; r , coefficient of correlation. Fixed data points of the equation were: SVL_{birth} , 33.6 mm and t_{birth} , 0 (see Materials and methods)

Population of origin	Sex	n	k	SVL_{max}	VR	r
Western	Males	74	0.205 (0.195–0.215)	83.2 (82.6–83.6)	88.93	0.94
	Females	46	0.184 (0.175–0.193)	85.2 (84.3–85.7)	93.22	0.97
Eastern	Males	140	0.296 (0.277–0.314)	83.6 (83.1–84.9)	41.33	0.64
	Females	92	0.173 (0.167–0.178)	94.9 (94.2–95.9)	69.55	0.83

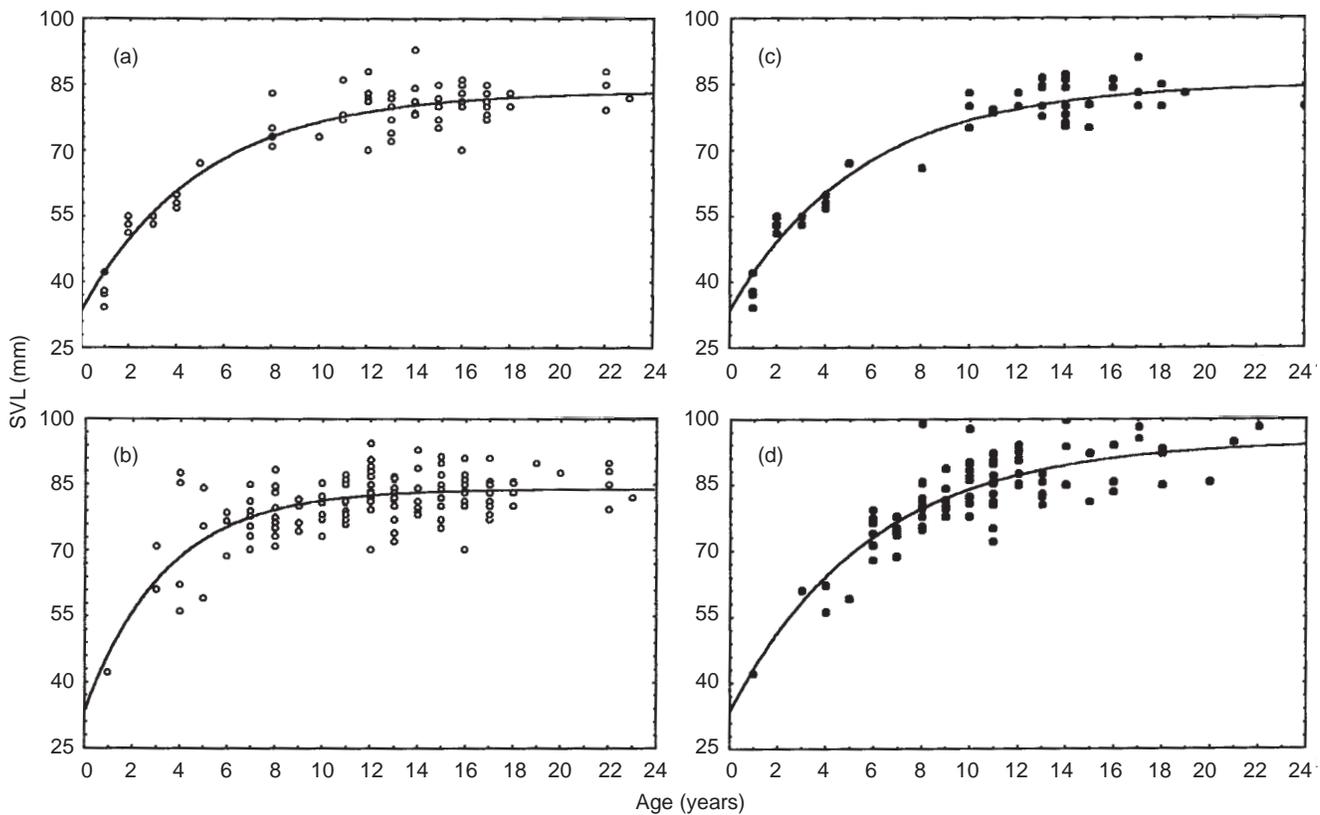


Fig. 3. Growth curves of males and females of the alpine salamander *Salamandra lanzai* from two neighbouring populations in the Cottian Alps: (a) males, western population; (b) females, western population; (c) males, eastern population; (d) females, eastern population. SVL, snout–vent length (mm). Parameters of growth curves are shown in Table 3.

Differences in age, size and growth

There are three main patterns for allocating food resources over the lifetime of a salamander (Bernardo, 1994): (1) allocation to reproduction only; (2) growth only for several years and then allocation to reproduction only; (3) growth only for several years and then allocate to reproduction and growth simultaneously. *Salamandra lanzai* growth curves resemble the third pattern. Growth and maturation are, in the temperate zone, under the constraint of an annual environmental cycle. In lizards, females become reproductively mature when they reach a threshold size and if it is the favourable time in the year (the ‘maturation window’: Adolph

& Porter, 1996). This constraint increases when the duration of the activity period or other resources decreases. The growth curve of the alpine salamander is relatively flat and such a pattern has also been observed in highland and high latitude populations of newts (Arntzen, 2000; Miaud, Guyétant & Faber, 2000).

In salamanders, males often mature earlier than females and at a smaller size (Tilley, 1973; Caetano, Castanet & Francillon, 1985; Miaud *et al.*, 1993; Rebelo & Caetano, 1995). In *S. lanzai*, this pattern was only found in the eastern population. Much of the variation between sexes could be explained by the fact that females need more stored energy as they need to allocate much more to gonad and embryo development than do

males (Halliday & Verrell, 1988). In the black salamander *S. atra*, adults matured at 4–5 years at 1700 m (Fachbach, 1988) and sexual maturity was delayed in both sexes until 10 years of age in alpine populations of the newt *T. alpestris* (Schabetsberger & Goldschmid, 1994; Miaud *et al.*, 2000).

Considerable interlocality variation in body size and age of salamanders has been documented (Tilley, 1973; Hairston, 1987; Miaud, 1992; Bruce, 1993; Caetano & Castanet, 1993; Miaud *et al.*, 2000). Such variation among populations could arise from several factors, i.e. genetic differences resulting from either selective pressures or genetic drift, and proximate differences in environmental conditions such as food availability. Several experimental studies of terrestrial ectotherms have shown a genetic (or other pre-hatching) basis for differences observed among populations. Differences between lowland and highland populations in size and patterns of growth in Iguanidae (Tracy, 1999), in age at maturity in a plethodontid (Bernardo, 1993), and in age and length at maturity in a frog (Berven, 1982), were shown to have a genetic basis. In *S. lanzai*, three juveniles caught in the western population and reared in the laboratory with an activity period of 8 months each year and food *ad libitum* matured at 3 years old (A. Ribéron, pers. obs.). This phenotypic plasticity has previously been described in life-history traits of amphibians: age at maturity in the newts *Triturus alpestris* (Schabetsberger & Goldschmid, 1994) and *Notophthalmus viridescens* (Gill, in Bernardo, 1993) and length at maturity in the salamander *Desmognathus ochrophaeus* (Bernardo, 1993) were determined by environment.

The proximate cause of variation among populations was attributed to food availability in amphibians and lizards (Fraser, 1976; Ballinger, 1977; Dunham, 1978). *Salamandra lanzai* is a carnivorous species and its foraging activity is only observed during or after rain both in the eastern (Andreone, Sindaco & Morisi, 1996) and western populations (Ribéron & Miaud, 2000). Because of the opportunistic carnivorous behaviour of this species (Andreone *et al.*, 1990), we hypothesize that food is not a limiting factor *per se* in both locations. The main difference comes from the frequency of the foraging opportunities, because the number of rainy days is 80% higher in the eastern site than in the western one. The length of time food is available, rather than its abundance, was argued to be of primary importance to Iguanidae (Tracy, 1999). Both age at maturity and mean size varies among these two alpine salamander populations. However, age seems to be more flexible because some males are able to reach maturity at only 3 years old and the youngest females were 6 years old in the more favourable environment, while both sexes reach maturity at a minimum age of 8 years in the other population. Larger mean length in the eastern population is reached with a higher growth rate. At the individual level, growth rates are not always maximized but rather are optimized (maximum *vs* optimum: Bernardo, 1994; Sibly & Atkinson, 1994). An optimum

growth rate would be a compromise between the benefit of attaining a particular size in a given amount of time and the cost incurred for rapid growth *per se* (Sibly & Atkinson, 1994). This compromise would be observed as a trade-off between growth rate and some other fitness traits (i.e. fecundity, juvenile mortality). This could be of particular importance in viviparous species, fitness of females being affected by the rate of conversion of energy into offspring, i.e. a two-stage process with the rate of acquisition of energy from the environment and the rate of conversion of acquired energy into offspring (Blackburn & Gaston, 1994). Moreover, the processes of gonad maturation rate and growth potential can be free to evolve independently (Bernardo, 1994), and this uncoupling would be of particular interest in *S. lanzai* where another difference observed among populations is the duration of gestation.

The study of more populations and more species is required to address the question on whether variation in life-history traits reflects local adaptation, displays geographic trends or is a function of phylogeny (Arntzen, 2000). Growing available genetic information in poikilothermic vertebrates will also afford unique opportunities to understand their evolution at the interface between molecular genetics, natural history and behavioral ecology.

Acknowledgements

This research was supported by the CEE Programme INTERREG 'Protection et valorisation touristiques des richesses naturelles du Queyras et du Val Pellice' and by the Region Rhône-Alpes Programme 'AVENIR, 1996'. We are grateful to Michel Blanchet, scientific supervisor in the Parc Naturel Régional du Queyras for assistance with the field and administrative work. P. Arntzen, D. Cogalniceanu, R. Griffiths, T. Halliday and A. de Ricqlès provided helpful suggestions on earlier drafts of this manuscript.

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