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## GEOGRAPHIC VARIATION IN BODY SIZE AND LIFE-HISTORY TRAITS IN BOSCA'S NEWT (*TRITURUS BOSCAI*)

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Body size of newts from five populations of *Triturus boscai* was measured and the age of the newts was estimated using skeletochronology. Variation in adult body size was observed throughout the range of the species, with largest individuals of the southernmost populations being smaller than the smallest adults of the northern localities. Sexual dimorphism in body size was detected in all populations studied. A tendency towards older mean ages was also observed from southern to northern populations. The age of youngest breeders, modal age at which growth slows, and mode of the age structure showed geographic variation, with the greatest differences in life-history traits being between northernmost and southernmost populations, survival being optimized in the north by delaying either the age of maximum reproductive output or sexual maturity. The variation observed may have been due to evolutionary changes, though more extensive information on genetic and morphological interpopulational differences is needed to support a taxonomic differentiation.

*Key words:* geographical variation, newt, life history, *Triturus boscai*

### INTRODUCTION

Geographic variation in body size is frequently associated with differences in several life-history traits throughout the range of a species, such as fecundity, age at maturity and longevity. These, in turn, may be associated with variation in morphological characteristics, such as body size and growth rate (Roff, 1992; Charlesworth, 1994).

Plasticity in phenotypic and life-history traits is not unusual in amphibians, and has been frequently reported to occur in urodeles (e.g. Hanken & Wake, 1993 and references therein; Tilley & Bernardo, 1993 and references therein; Kalezic, Cvetkovic, Djorovic & Dzukic, 1994). In some cases the variation is supported by genetic differentiation resulting from adaptive plasticity through evolutionary processes, while in other cases non-adaptive plasticity is observed, and the variation may be regarded as a response to local environmental characteristics (Bernardo, 1994).

In urodeles, and in particular in the genus *Triturus*, a decrease in body size has been observed for certain species throughout their range, occurring mainly under extreme environmental conditions (Beebee, 1983; Dolmen, 1983; Díaz-Paniagua, Mateo & Andreu, 1996). The small body size in some *Triturus* populations has led to the description of different taxonomic groups (Wolterstorff, 1905; Raxworthy, 1988; García-Paris, Herrero, Martín, Dorda, Esteban & Arano, 1993). A small body size confers some advantages to individuals, as it reduces nutritional requirements (Clarke, 1996) and their maintenance costs (Bernardo, 1994). Size reduction is normally associated with variation in life history traits such as

fecundity, age at maturity, longevity and reproductive life span (e.g. Roff, 1992).

*Triturus boscai* is an endemic species from the western half of the Iberian Peninsula, and is considered to be closely related to other small-bodied *Triturus* species (e.g. Macgregor, Sessions & Arntzen, 1990; Halliday & Arano, 1991). No subspecies have been described for *T. boscai*. However, variability in colouration (Malkmus, 1980-81) and genetic patterns (Herrero, 1991; Arano, Herrero, García-Paris, Mateo & Sanchíz, 1997) have been reported throughout the species range, and substantial differences in adult body size among populations are evident from studies from different localities (Malkmus, 1980-81; Caetano, 1982). The aim of this paper is to describe the variability in adult body size and some life history traits in *T. boscai* along a north-south gradient across its geographic range. The observed variation constitutes an interesting basis for *a posteriori* analyses of taxonomic differentiation including a more extensive study on morphological and genetic differentiation among populations.

### METHODS

We analyzed the characteristics of newts from five populations located along a latitudinal gradient across the range of the species, which can be classified as: northern populations: Pontevedra-Bueu (P), Lugo-Ancares (L); central population: Salamanca-Candelario (S); and southern populations: Huelva-Aroche (H), Huelva-Doñana (D) (Fig. 1). A description of the main characteristics of each locality is given in Table 1.

Individuals from all localities, except D, came from the scientific collection of the Estación Biológica de Doñana (CSIC), and all were mature newts collected during the aquatic phase within one breeding season in each locality. Newts from D were live individuals, captured during the breeding season of 1994 and 1995, which were released in the field after being measured

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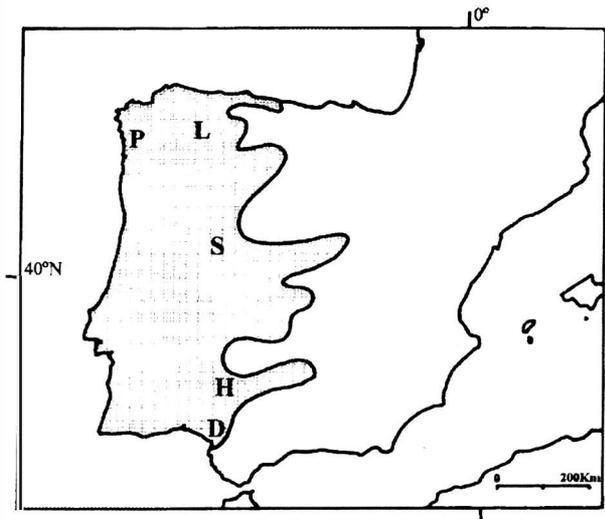


FIG. 1. Locations of sampling sites within the range (shaded area) of *Triturus boscai*.

and weighed. We clipped and preserved one toe for age determination from each of 60 individuals. The absence of preserved newts from D forced us to compare their measures with those from preserved individuals, which may have contributed towards an increase in the observed differences, mainly because of a wider variation in the measures recorded for D newts. We assumed, nevertheless, that the data satisfactorily reflect the range of body length within each population, although some distortion may be expected in preserved specimens (Verrell, 1985).

As measures of newt size we recorded: (a) body length (BL) from the snout to the anterior tip of the cloaca; (b) body plus vent length (SVL) from the snout to the posterior tip of the cloaca; and (c) total length (TL) from the snout to the tip of the tail. These were recorded with vernier callipers to the nearest 0.5 mm. SVL and TL are given to enable comparisons with other studies. Because SVL may show wide variations

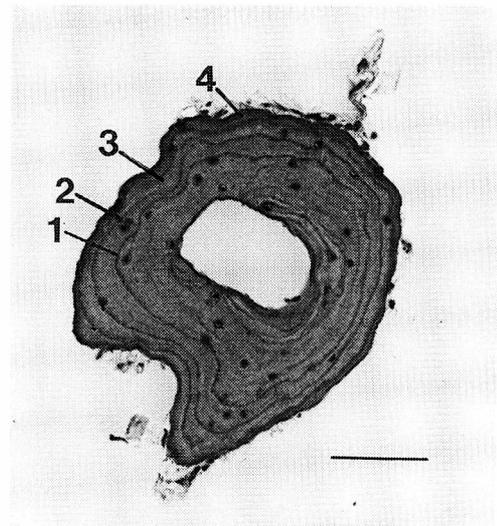


FIG. 2. Stained sections of a humerus of a male *T. boscai* from S, showing 4 LAG (1 wide band + 2 medium bands + 1 narrow band + the last incomplete band) and PAM = 2 yr. Scale bar = 100  $\mu$ .

depending on the sex and on the reproductive stage of individuals, and the tail is frequently broken or regenerated, we used only BL in comparisons between populations.

We estimated the age of newts by skeletochronology (see Fig. 2). Sections of decalcified humeri of preserved newts were obtained with a freezing microtome and stained with Ehrlich's hematoxylin (see details of the technique in Castanet, 1982; Leclair & Castanet, 1987; Castanet & Smirina, 1990). Following Caetano, Castanet & Francillon (1985), Francillon-Viellet, Arntzen & Géraudie (1990) and Miaud (1991), we considered the lines of arrested growth (LAG) to correspond to periods of inactivity, while the zones of bone layers between LAG (hereafter referred to as bands) correspond to the periods of activity and growth (Caetano *et al.*, 1985; Verrell & Francillon, 1986; Miaud, 1991; Caetano & Castanet, 1993). Growth bands should therefore form annually, as demonstrated

TABLE 1. Main characteristics of the five localities of newts considered in this study, listed from south to north. Temperature ( $T^a$ ) data for H, S, L and P come from Montero & Gonzalez (1983). (See Material and methods for complete locality names).

Locality	Altitude	Rainfall	July $T^a$	Jan $T^a$	Substrate	Vegetation
D	10-20 m	585 mm	24.5°C	10.6°C	Sandy	Mediterranean shrubland
H	350-500 m	832 mm	25.3°C	7.7°C	Plutonic	<i>Quercus</i> and <i>Eucalyptus</i> woods with Mediterranean shrubland
S	1000-1050 m	1111 mm	22.6°C	5.5°C	Plutonic	<i>Quercus</i> woods with Mediterranean shrubland
P	10-60 m	1727 mm	20.0°C	9.0°C	Plutonic	<i>Eucalyptus</i> spp. forests with Mediterranean shrubland
L	800-1100 m	1901 mm	15.3°C	1.2°C	Siliceous	Clear <i>Quercus</i> and <i>Castanea</i> woods with Mediterranean shrubland

TABLE 2. Mean and standard deviation of snout-vent length, body length, total length, and mass of *T. boscai* from five localities along a latitudinal gradient across its distribution range (body mass of fresh specimens were only available from D and S).

		Body length (mm)			Body+vent length (mm)			Total length (mm)			Body mass (g)		
		Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>
D	Male	24.9	2.26	93	25.1	2.24	22	45.2	3.78	38	0.47	0.05	93
	Female	26.0	2.43	61	27.2	4.73	16	55.0	4.53	31	0.58	0.16	61
H	Male	28.2	1.31	40	32.7	1.57	25	66.1	3.12	40	1.14	0.33	40
	Female	34.0	1.59	37	37.2	2.61	37	72.8	3.90	37	1.51	0.42	37
S	Male	28.1	1.67	33	32.1	2.1	33	63.0	3.87	33	-	-	-
	Female	34.1	1.49	37	36.9	1.59	37	72.7	4.31	37	-	-	-
L	Male	30.7	1.33	29	35.1	1.56	29	66.7	3.87	29	-	-	-
	Female	37.0	3.27	33	40.4	2.35	33	79.3	3.99	33	-	-	-
P	Male	32.0	1.40	26	36.3	1.63	26	68.9	3.53	26	-	-	-
	Female	39.0	2.09	37	41.9	1.99	37	81.8	4.06	37	-	-	-

for the sympatric and congeneric species *Triturus marmoratus* by Caetano (1990). In newts from D, the same technique was used in phalanx sections. We confirmed the same number of bands in humeri and phalanges of 14 preserved individuals (6 from D, 6 from S, 2 from L). Caetano (1990) confirmed the same number of LAG in humeri and in phalanges of *Triturus marmoratus*, and Marnell (1997) obtained similar results in a small-sized newt, *Triturus vulgaris*. Double lines were detected in a small percentage of individuals from different localities and they were considered as corresponding to one year with several shorter inactivity periods (e.g. Caetano, 1990).

The relationship with body size was analysed by considering the number of bands rather than LAG, in order to differentiate the newts captured at the beginning of the activity period from those recorded after growing during the activity season. We did not consider 5.2% of 286 individual stained bone sections (2.1% from D, 1% from H, 1.75% from L and 0.35% from S), because LAG were not clearly visible or the zone of endosteal resorption was too large, which could have affected the number of LAG estimated.

The age at maturity is commonly considered to be associated with a decrease in the growth rate and some authors have considered it to correspond with the age when LAG become closer (Leclair & Castanet, 1987; Mateo & Castanet, 1994), although for some newt populations sexual maturity has been demonstrated to occur before the age of growth decrease (Francillon-Viellet *et al.*, 1990). In this study, the irregularity of the bands, especially those of phalanges, prevented precise width measurement. Therefore, we classified bands in three relative width categories (wide, medium and narrow), and considered that the growth rate decreased when narrower bands appeared

after wide or medium ones. The number of wide bands was assumed to correspond with the probable age at maturity (PAM hereafter). PAM was considered only for newts showing a decrease in growth rate. We compared the modes of PAM distribution with the modal and minimum classes of the age distributions for each breeding population.

Differences in body size and age distributions were analysed by means of two way ANOVAs in which the effects of locality and sex were tested. Student-Newman-Keuls *a posteriori* tests were employed with one way ANOVAs.

## RESULTS

A significant variation in body size was observed for *T. boscai* throughout its range ( $F_{4,272} = 569.5$ ,  $P < 0.001$ ) (Table 2). The smallest newts were observed in the southernmost populations, from Doñana National Park (D). These averaged 24.9 mm and 26.0 mm in BL (males and females respectively) while the newts from H, about 50 km to the north, were about 4 mm (males) and 8 mm (females) longer on average. In the centre of the range, in S, the newts did not significantly differ in size from H (after Student-Newman-Keuls *a posteriori* test), with an average BL of 28.2 mm and 33.9 mm for males and females, respectively. They also differed from newts from northern populations: in L, males averaged 30.7 mm and females 37.0 mm; and in P, 32.0 mm and 39.0 mm respectively (Table 2).

Sexual dimorphism also contributed to interpopulational differences, as reproductive males were significantly smaller than reproductive females ( $F_{1,272} = 320.19$ ,  $P < 0.0001$ ) in each locality. However, the difference between BL of males and females was much smaller in newts from D than in the other localities (Table 2).

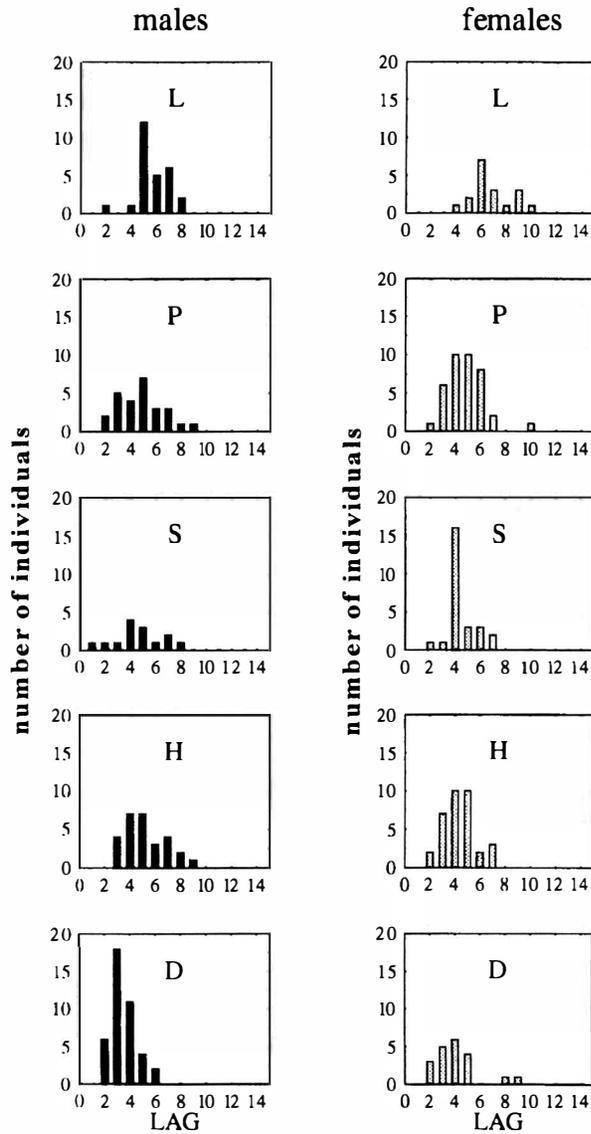


FIG. 3. Age structure of male and female newts in the five populations studied. Age is expressed as the number of lines of arrested growth (LAG) counted in bone sections.

The age structure also varied significantly among populations ( $F_{4,260} = 16.99, P < 0.0001$ ), with older mean ages tending to be observed in the northern populations (Fig. 3). Mean age of reproductive newts varied from 3.5 LAG in D to 5.6 in L (males), and from 4.1 LAG in D to 6.8 LAG in L (females). No differences were observed between age distributions of males and females within populations, except in L ( $F_{1,45} = 5.84, P = 0.0198$ ).

Maximum longevity was registered for a female from L, with 10 LAG, and a male from P, with 9 LAG. However, there did not appear to be any consistent differences in longevity between the sexes (Fig. 3).

Regarding the youngest breeding individuals, one male from S was aged 1 yr, while all males were over 2 yr in P and D, and over 3 yr in H. It is remarkable that the age distributions did not show decreasing frequencies from lower to higher age classes, but instead displayed two-tailed distributions (Fig. 3). The modal age class varied among populations according to the latitudinal gradient, from 3 yr in males from D, to 6 yr in females from L. In these two populations the modes corresponded with older age classes in females than in males, females also achieving greater longevity. In the remaining populations, males and females had similar modal ages and a higher frequency of males was observed in the older age classes. The difference between the age of the youngest breeding individual and the mode differed among populations from one year in males from D and H to three years in newts from L, P and S (Fig. 3).

Body size was not significantly correlated with age in any population, a wide range of body sizes being observed for most age classes (Fig. 4). The largest males and females from D were both smaller than the smallest individuals of the same sexes at any other locality. Mean body size of 3 yr males from D was about 5 mm smaller than in similar aged males from S and H, and 9 mm smaller than the mean size of P newts. Even larger differences were observed for females: mean body size of all age classes from D was about 7 mm smaller than mean BL in other populations. On average, 4 yr old females from D were 15.4 mm smaller than 2 yr old females from L.

Most bone sections exhibited wide bands corresponding with the earliest ages, followed by medium or narrow bands which were assumed to correspond to post-maturation years with lower annual growth rates. Table 3 shows the number of individuals in each population showing 1, 2, 3 or no bands formed before the decrease in growth rate occurred (through the detection of subsequent narrow bands).

A small percentage of breeding males from D, H, L and P showed no wide bands, probably indicating that they had matured during the first activity period after metamorphosis (PAM = 1). All males (except one from D) also exhibited one to six medium bands, possibly

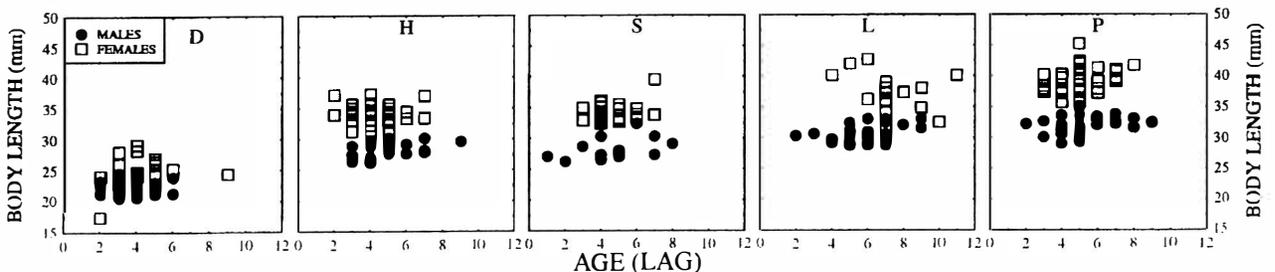


FIG. 4. The relationship between age (number of LAG) and body length (imm) of newts in the five populations studied.

TABLE 3. Number and percentage (in parentheses) of individuals with 0, 1, 2 or 3 wide bands formed in bone sections before medium or narrow bands, indicative of the age of growth decrease (only individuals presenting narrower bands after wide bands were considered). The percentage of individuals with double lines (DL) is also shown.

	Males					Females				
	No. wide bands					No. wide bands				
	0	1	2	3	DL	0	1	2	3	DL
D	6 (27.3)	15 (68.2)	1 (4.5)	0	0	1 (6.3)	15 (93.7)	0	0	3.02
H	6 (25)	9 (37.5)	9 (37.5)	0	32.0	3 (9.4)	10 (31.2)	16 (50)	3 (9.4)	5.9
S	0	4 (44)	5 (55)	0	7.1	0	11 (44)	12 (48)	2 (8)	7.4
L	3 (12)	15 (60)	7 (28)	2 (7.4)	38.9	10 (58.8)	6 (35.3)	1 (5.9)	0	25
P	2 (8.7)	12 (52)	9 (39)	0	8.3	3 (9.6)	9 (28.1)	17 (53.1)	3 (9.3)	7.7

corresponding to medium growth before or after maturity. More than 50% of males in D, L and P showed one wide band, probably corresponding to sexual maturity during the second year of life (PAM = 2 yr). In H, a similarly high proportion of one and two wide bands comprised up to 75 % of cases. All individuals from S had one or two wide bands, suggesting that PAM = 2 or 3 yr. In L and P a small percentage of males had three wide bands (PAM = 4 yr). Double lines were observed in all populations except in D (Table 3).

A small proportion of breeding females in D, H and P presented no wide bands, but showed up to three medium bands, indicating a relatively low growth rate during their first years of life. In L, a high proportion of females did not exhibit wide bands, with a maximum of three medium bands. All females from S had more than one wide band (PAM > 1 yr). In D, 93% of females showed only one wide band (PAM = 2 yr), while in S and H, high percentages were similarly distributed between one and two wide bands. A small proportion of females with three wide bands (PAM = 4 yr) were found in H, S and P. Double lines were observed in all populations, most frequently in L and D (Table 3).

#### DISCUSSION

*Triturus boscai* shows a latitudinal variation in body size which may have important implications, such as the prevention of interpopulational mating, considering that body size may influence sexual selection (Halliday & Verrell, 1986; Verrell, 1989). The populations from S and H did not differ widely, despite the large distance that separates them. The highest variation was observed in the populations located close to the northern and southern limits of the range of the species. The very small body size of D newts, especially males, indicates that this population is considerably isolated and differentiated from the nearby population at H. D is located at the southern limit of the species range, where the sympatric species *Triturus marmoratus pygmaeus* displays a similar variation in body size (Díaz-Paniagua *et al.*, 1996), suggesting that the characteristics of the biotope favour the attainment of small adult body sizes, as Hanken & Wake (1993) commented for certain environments. Although it is not demonstrated which

environmental characteristics at D favour the diminution of body size, several habitat features, such as low annual rainfall and temporary ponds with a long desiccation period, coincide with those of habitats of other small subspecies of *Triturus* (Raxworthy, 1988).

Sexual dimorphism was also evident in body size, and contributed to an increase in the differences between populations. Geographic variation in sexual size differences has also been reported in other species of *Triturus*, and was explained as a consequence of population specificity in sexual growth rates (Kalezic, Crnobrnja, Djorovic & Dzukic, 1992). The ratio of sexual size dimorphism was smallest for D newts, which may be a further consequence of the particular ecological characteristics of this area.

The latitudinal variation in body size corresponded with the variation in age structure. In a previous study, Caetano (1990) observed that populations of *T. boscai* from southern and northern Portugal, and from low and high altitudes, did not differ in age at maturity, reaching a maximum longevity of 7 to 8 years. In our study we have considered populations of a wider latitudinal range, and, although we agree with Caetano (1990) in general aspects, we have found variation in both parameters, mainly between the most extreme populations, which are out of the range studied by Caetano (1990). Although this author, based on the spatial pattern of LAG, found that newts reached maturity at 3 yr, in our study the minimum age of mature newts was 2 yr in most populations.

It is remarkable that the age structure in all studied populations did not show a decrease from younger to older age classes. In a study on three other *Triturus* species Miaud (1991) described decreasing age structures for females, while male frequencies decreased only from the second age class on. His interpretation was that most individuals matured at the modal age class. In the present study we found that the modal age class of *T. boscai* was from one to three years higher than the minimum age of breeding newts, and did not coincide with the mode of PAM distribution. This difference may be explained by the possibility of lower reproductive frequencies of younger adult newts, which could be associated with the relatively high frequency of indi-

viduals with medium instead of wide initial bands. A lower than annual reproductive frequency in a portion of the population is not uncommon in *Triturus* and has been proposed previously for *T. vulgaris* in an urban population from England (Griffiths, 1984) and for females of *T. marmoratus* from D (Díaz-Paniagua, 1998).

The modal age class seems to be population specific. As occurred with body size, mean age of breeding individuals was higher in northern (L and P) and lower in southern populations (D). This is probably associated with a delay in sexual maturity and/or a decrease in reproductive frequency of younger individuals, which is likely to have important repercussions in life history traits such as fecundity, survival and longevity within each population (e.g. Stearns, 1976; Roff, 1992). The differences observed suggest that at least northernmost and southernmost populations have different life history traits, northern populations optimizing survival of individuals by delaying the age at maturity and/or the seasons of maximum reproductive output, whereas in the central and southern populations a higher reproductive investment occurs in the earlier years, resulting in lower survival probabilities and reduced longevity.

As observed in other urodeles (Halliday & Verrell, 1988), body size of *T. boscai* cannot be considered a reliable predictor of newt age. Age and body size were not correlated in any population, and we even found negative tendencies, with smaller individuals in the older age classes. This may be explained by the drastic decrease of growth rates after sexual maturity is attained, as well as by the different interannual reproductive effort of individuals, resulting in different individual growth trajectories.

The variation in reproductive investment in the early age classes may not be the cause of the differences in body size observed among populations, since all individuals from the southernmost population were smaller than the youngest from the northern populations. Therefore, sexual maturity is reached at different body sizes in populations from different localities, independently of age. Differences in age at maturity and growth rate were detected in two populations of the salamander *Desmognathus ochrophaeus*, where the variation in growth was found to be dependent on environmental factors, while age at maturity was established genetically, suggesting that both parameters may evolve independently (Bernardo, 1994).

In other *Triturus* species variation in body size has been considered to characterize different taxonomic groups within species, as is the case of the dwarf subspecies of smooth newts, *T. vulgaris schmidlerorum* from Turkey (Raxworthy, 1988), and *T. marmoratus pygmaeus* in the southern half of the Iberian Peninsula (García-Paris *et al.*, 1993). The variation in body size of *T. boscai* has a geographic basis and occurs between distant populations which have evolved different life history traits. However, more information on the genetic and morphological variation among populations is needed to identify taxonomic differentiation.

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