AGE, BODY SIZE AND GROWTH OF *LACERTA AGILIS BOEMICA* AND *L. STRIGATA*: A COMPARATIVE STUDY OF TWO CLOSELY RELATED LIZARD SPECIES BASED ON SKELETOCHRONOLOGY

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Age and growth in *Lacerta agilis* (ssp. *L. a. boemica*) and a closely related sympatric species *L. strigata* from the eastern North Caucasus, Russia were assessed by skeletochronology and back-calculation methods. We examined 320 specimens from one lowland, two submontane (both species), and two mountain (*L. agilis*) localities. Age structure, back-calculated snout-vent length (SVL) at hatching and subsequent hibernations, and asymptotic SVL were studied for sexual dimorphism, altitudinal variation and interspecific differences. Pattern of resorption of growth layers in bone and its possible effects on growth inferences from skeletochronological data were also considered. The back-calculated SVLs showed a good conformity to comparable field data. Mean and maximum SVL at the first hibernation clearly decreased with altitude. Within the same localities, these parameters were consistently higher in *L. agilis* than in *L. strigata*. Between the 1st and 2nd hibernations (the period of the highest increment in SVL in all study populations), *L. strigata* grew faster than the syntopic *L. agilis*. In the lowland locality, females of both species tended to grow slower than males between the 1st and 2nd hibernations, while at higher elevations they exhibited lower SVL increments than the males between the 2nd and 3d hibernations. This pattern, along with occurrence of gravid yearlings in the lowland locality (but not in the other sites), suggests an earlier onset of reproduction in the lowland populations compared to those from higher elevations. Asymptotic SVLs in the study populations tended to be larger in males than in females. In *L. agilis* these sexual size differences (SSD) varied among populations, being quite strong in the lowland site and negligible at the highest locality. The mountain populations (960 and 1900 m a.s.l.) of *L. a. boemica* exhibited higher mean age and longevity than the lowland and submontane populations (20-600 m a.s.l.) of both species; however, no clear altitudinal trend was found for adult SVL. Much of the variation revealed in this study, including the interlocality differences in SSD, can be related to the length of activity season, in line with recently published theoretical models and experimental studies stressing the role of proximate factors.

Key words: altitudinal variation, asymptotic size, life-history, lizards, sexual size dimorphism

INTRODUCTION

In recent decades lizards have become model organisms for studying factors determining variation of life-history and demography traits within and among species (Pianka & Vitt, 2003). An advanced theoretical and methodological framework has been developed in this field providing estimates of the relative importance of evolutionary constraints (Dunham *et al.*, 1988; Bauwens & Diaz-Uriarte, 1997), genetic adaptation and phenotypic plasticity (e.g. Grant & Dunham, 1990; Adolph & Porter, 1993, 1996; Niewiearowski & Roosenburg, 1993; Qualls & Shine, 2000; Lorenzon *et al.*, 2001). These studies have mostly been confined to a small set of populations and taxa (North American iguanids, a few species of Australian skinks and West European lacertids). The problem is that both mark-recapture and experimental studies – the main tools used to obtain data on growth and longevity – are very time-consuming.

A reasonable alternative tool to obtain such data arise from life-history investigations based on counting and measuring growth layers in the bone or other hard tissues (Mina & Klevezal, 1970). The formation of these layers reflects the seasonal changes of the growth rate of an animal. This method, known among herpetologists as skeletochronology (Castanet *et al.*, 1977), provides not only accurate age determination in reptiles and amphibians (Smirina, 1972; Castanet *et al.*, 1977; Castanet & Smirina, 1990) but also a quantitative estimation of the pattern of bone growth (Castanet & Baez, 1991; Bruce *et al.*, 2002; Sinsch *et al.*, 2002; etc.). Due to a generally high correlation between the bone thickness and body size, body size at the time of formation of a corresponding growth mark can be back-calculated from the size of the growth mark, current body size and current bone thickness. Such retrospective estimation of body size at specific ages is a common practice in fish studies (Francis, 1990). This procedure was also used on amphibians (e.g. Smirina, 1983; Marunouchi *et al.*, 2000), but,

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with the exception of one study on turtles (Sergeev, 1937), it has not yet been applied to reptiles.

The objective of the present study was to comparatively examine altitudinal variation and sex differences for age structure, asymptotic body size and growth pattern in two related syntopic lizard species from the Caucasus. The data were obtained from preserved specimens using skeletochronology and back-calculation methods. As the back-calculation technique had never before been applied to squamate reptiles, particular attention was given to the methodological problems that can arise through inferences about body growth from skeletochronological data.

MATERALS AND METHODS

STUDY SPECIES

L. agilis and *L. strigata* are medium-sized, diurnal, insectivorous lizards of the family Lacertidae. They are closely related (although non-sister) species belonging to the subgenus *Lacerta s. str.* (= *Lacerta I* group *sensu* Arnold, 1989). *L. agilis* occupies a larger part of the temperate zone of the Palaearctic from southern England and the Pyrenees in the west to the Baikal Lake in the east (Bischoff, 1988), and *L. strigata* inhabits the eastern Caucasus and adjacent parts of Turkey and Iran (Darevskij, 1984). In the eastern Caucasus, *L. agilis* and *L. strigata* are broadly sympatric and often coexist in the same habitats (Roitberg, 1982), providing an opportunity for a comparative study of two species in a common range of environmental conditions. Daghestan (the south-eastern North Caucasus) seems particularly promising for such studies due to considerable landscape/climatic heterogeneity within a small area. Moreover, *L. agilis* is represented here by a very peculiar subspecies, *L. a. boemica* whose coloration, scalation and body proportion features make it the most similar to the other related species (*L. strigata*, *L. viridis*, etc.) and the most distinct phenetically, compared to the other subspecies of *L. agilis* (Roitberg, 1987). According to a recent molecular-genetic study (Kalyabina *et al.*, 2001) *L. a. boemica* also exhibits a strong separation from the rest of the species occupying a basal position in the species phylogeny.

STUDY SAMPLES AND COLLECTION SITES

Our study material comprised 540 specimens from five *L. a. boemica* populations and three *L. strigata* populations; 320 of them (all adults and the largest subadults) were used for skeletochronological analysis (Table 1). No animals were sacrificed for this study. We used only preserved specimens that had already been collected for other purposes (Roitberg, 1982, 1987, 1989, etc.). The specimens originate from five localities (sites) in the lowlands (Kostek), submontane (Sergokala, Khuchni) and montane (Termenlik, Kuli) regions of Daghestan (Appendix 1). In Kostek, Sergokala and Khuchni the two species live syntopically and were sampled from the same collection sites. In Termenlik and Kuli *L. strigata* did not occur.

AGEING AND MEASURING GROWTH MARKS

The annual pattern of growth layer deposition in bone was validated experimentally for various reptilian and amphibian species living in temperate climates (Smirina, 1972; Castanet *et al.*, 1993), including the lizard *Lacerta bilineata* (=*L. viridis*) (Castanet *et al.*, 1993). Since *L. bilineata* is closely related to our study species (Arnold, 1989) and the winters in the North Caucasus are not milder than in West Europe, we are greatly confident that the number of resting lines (=lines of arrested growth, or LAGs - Castanet *et al.*, 1977) corresponds to the number of hibernations experienced by the individual. The LAGs were counted on transverse sections of the middle part of femur diaphysis, the growth pattern was assessed by measuring bone diameters limited by consecutive LAGs (Fig. 1). Each femur bone was decalcified in 5% nitric acid solution, cross sectioned (20-25 μm thick) with a freezing microtome and stained with Ehrlich haematoxylin. Diameters limited by consecutive LAGs and by the outer bone margin $(D_1, D_2 \dots D_n, D)$ were measured with ocular-micrometer under a light microscope. As the contours of the bone sections deviate from a true circle, means of the minimal and maximal diameter (Fig. 1), measured in three sections from every specimen, were used to estimate the bone width at the time of a LAG formation and at capture. The word "diameter" is used here as a workable quantification of bone thickness and not as a strict geometric term.

For nearly all the femurs examined, LAGs were well defined providing precise age estimation. Additional and double lines (Castanet & Smirina, 1990) did occur but were easily recognisable. Only two femurs gave some difficulties in age estimation but the possible error margin did not exceed 1 year.
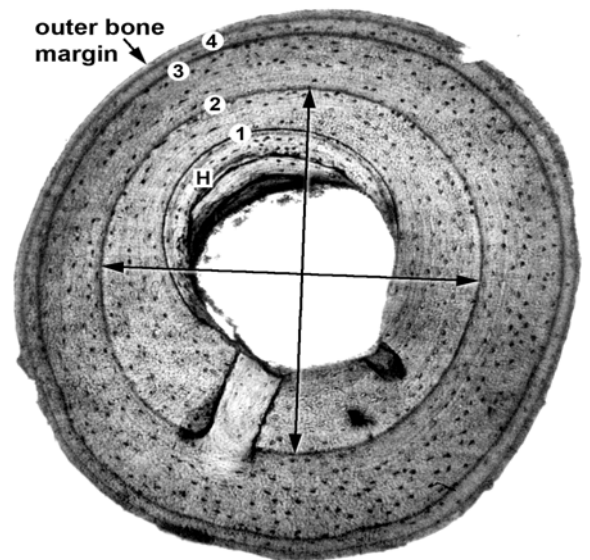

FIG. 1. Cross section of the femur diaphysis of *Lacerta agilis boemica* (adult male from Kuli). Ehrlich hematoxylin; magnification: ob. 6.3, oc. 3.2. H - hatching line; 1-4 - LAGs (= resting lines) of consecutive hibernations; arrows inside the section show the minimal and the maximal diameters of the bone limited by LAG2.

BACK-CALCULATION PROCEDURE

A high correlation between SVL and femur diameter (0.84-0.98 in our study samples – Roitberg & Smirina, 1995, 2005; see also Castanet & Baez, 1991; Arakelyan, 2002) made it reasonable to perform back-calculation of individual body length at the time of each LAG formation (hatching and subsequent hibernations). Different back-calculation formulae (BCFs) have been proposed and used for back-calculating body size from the size of a growth mark (Francis, 1990; see also Marunouchi *et al*., 2000). The simplest BCF, the Dahl-Lea formula, is merely a proportion: $L_i = L_c(D_i/D_c)$, where L_i and L_c are snout-vent lengths at the time of formation of the ith LAG and at capture; D_i and D_c are the bone diameters limited by LAG_i and by the outer bone margin, respectively. The other BCFs also incorporate, along with L_c, D_i and D_c, parameter(s) of a regression of L on D (or D on L) in the corresponding population (Francis, 1990). The only but quite powerful validation study made on an ectotherm tetrapod (the frog *Rana japonica*) showed that all eight BCFs tested tended to overestimate the actual SVL at the previous capture (Marunouchi *et al*., 2000). Surprisingly, the simple Dahl-Lea BCF provided the best estimation (mean deviation +0.6, SD 2.8 mm) (Marunouchi *et al*., 2000). This BCF was used in the present study.

Another advantage of the Dahl-Lea BCF is that it does not require calculation of the regression parameters. A reliable estimation of these parameters can encounter substantial problems as the corresponding sample should not only be large enough, but should also cover the entire population size range (if the latter is not the case, the estimates might become biased: Ricker, 1973; Francis, 1990). These requirements could be fulfilled by pooling conspecific samples from different localities. However, in the study species the relationship between the body length and bone thickness did differ among localities (Roitberg & Smirina, 2005) making locality pooling inappropriate.

ESTIMATING ASYMPTOTIC LENGTH

Using nonlinear regression techniques, two asymptotic growth models were fitted to our age-size data for each combination of population and sex: the von Bertalanffy model $L_t = A - (A - L_0)e^{-k(t-t_o)}$ and the logistic-by-length model $L_t = A/[1+(A/L_0-1)e^{-k(t-t_o)}]$, where *e* is the base of the natural logarithm, t is age (number of growing seasons experienced), t_o and L_0 are age and length at the start of the growth interval under study, A is the (average) asymptotic SVL (in mm), k is the characteristic growth rate. These two models for linear growth are the ones most commonly encountered in studies on reptiles (Andrews, 1982; James, 1991; Kratochvil & Frynta, 2002). Taking into account the scarcity of our data on the size at hatching (SVL_0) which is usually taken as L_0 (Andrews 1982; Kratochvil & Frynta, 2002), we chose mean SVL_1 and $t_o = 1$ (length and age at the first hibernation) as initial values of the above growth models. Doing so might have an additional advantage since the time of entering the first hibernation is probably less variable than the hatching time, at least within populations.

In most of the samples, the von Bertalanffy model explained a slightly higher percentage of variance than the logistic model, and so was used to estimate the asymptotic SVL for all sites.

As sample estimates of the growth curve parameters can be sensitive to the structure of original data (see Discussion), we also used another estimate of the asymptotic body length, namely the 80 percentiles of the SVL distributions of adult animals (Brown *et al*., 1999). In a mark-recapture study on the agamid lizard, *Agama impalearis,* this simple statistic exhibited a good conformity with growth-based estimations (Brown *et al*., 1999).

STATISTICAL ANALYSIS

Operational units of statistical comparisons in this study were samples of specimens of the same species, the same sex and collected from the same locality. We designated these as study samples. Subsamples of individuals collected in different years were pooled for all analyses.

All data were tested for normality (Shapiro-Wilk *W*-test) and for homogeneity of variances (Levene test, Liliefors). Both parametric and non-parametric statistics were used for the analysis depending on the distribution type of the variable (Sokal and Rohlf, 1995). For multiple comparisons, we considered only those individual differences, which remained significant ($P<0.05$) after the sequential Bonferroni adjustment (Rice, 1989). We used SPSS 11.0 for all the analyses.

TABLE 1. Study sites and sample sizes. Values shown are the number of specimens used for skeletochronology, with overall sample size in parentheses.

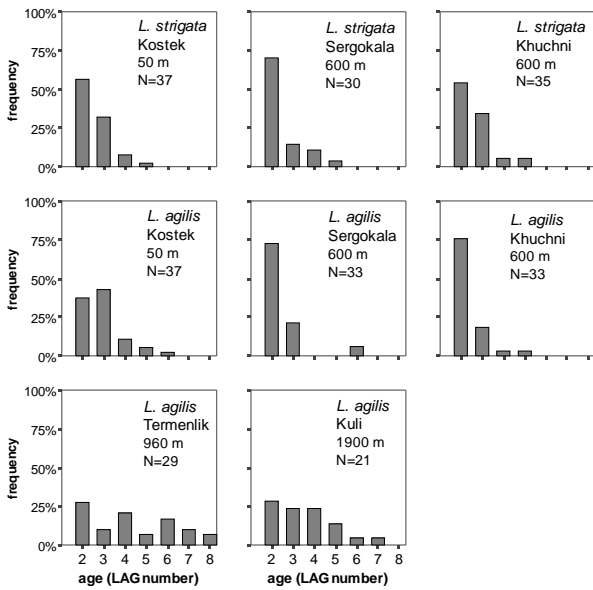| Locality	Capture dates	*L. a. boemica*		*L. strigata*	
		males	females	males	females
1. Kostek	April-September 1984-85	24 (41)	30 (45)	26 (37)	21 (28)
2. Sergokala	11-14 June 1982	19 (35)	18 (34)	14 (31)	13 (37)
3. Khuchni	9-14 July 1985, 5-8 June 1986	28 (35)	25 (36)	26 (35)	24 (43)
4. Termenlik	April-September 1981-85	22 (23)	29 (32)		
5. Kuli	July 1992-93	10 (13)	13 (15)		

FIG. 2. Age (yr) distribution in adult samples of *L. a. boemica* and *L. strigata* from five different localities of the eastern North Caucasus. Locality elevations are given within the plots.

RESULTS

AGE STRUCTURE

In seven out of eight study populations, the proportion of yearlings to the total sample (yearlings + adults) was 43-56%. In the Kuli sample (the highest elevation) yearlings constituted only 22%. This proportion did not differ significantly between sexes. Age distributions in the samples of adults are presented in Fig. 2. Preliminary examination for sex differences had revealed only one significant value (*L. strigata*, Khuchni: $P=0.012$, Mann-Whitney test) in eight comparisons which became non-significant after Bonferroni correction. Therefore, sexes were pooled for further analysis. No significant differences were detected between syntopic populations of *L. a. boemica* and *L. strigata* within localities ($P>0.05$ in all three sites).

Two mountain *L. agilis* populations differed from the foothill and lowland populations of both species in having a large proportion of older animals and higher

maximum age (Fig. 2). The latter were 7-8 years in the mountain localities and 5-6 years at the other study sites. Kruskal-Wallis tests revealed significant interpopulational differences for age structure in *L. agilis* (for all localities: $\chi^2=35.8$, df=4, $P<0.001$; for the non-mountain localities: $\chi^2=9.9$, df=2, $P=0.007$), but not in *L. strigata* ($\chi^2=2.0$, df=2, $P=0.38$). Pairwise comparisons detected that the two mountain *L. agilis* populations did not exhibit significant difference from one another (Mann-Whitney test, $P>0.2$), but did differ from nearly all the other study populations. The lowland *L. agilis* population differed from both submontane *L. agilis* populations ($P<0.02$, Mann-Whitney test). To summarise, the age structure of the mountain *L. agilis* populations showed a clear shift to older ages as compared to the submontane populations, with the lowland *L. agilis* exhibiting an intermediate state.

PATTERN OF GROWTH MARKS RESORPTION

Resorption rates of the first two LAGs in the eight study populations, estimated as proportions of individuals in which the corresponding LAG diameters could not be measured, are given in Table 2 (as no consistent sex differences within populations were detected, males and females were combined for further comparisons). For LAG1, the resorption frequency was negligible for yearlings (0-10%) and increased dramatically for 2-yr-old lizards (up to 80-90% in some populations). However, animals that were at least 3-years old generally exhibited only a slight (if any) increase in the resorption frequency as compared to the 2-yr-olds from the same population (Table 2).

The resorption frequency for LAG1 in adults varied substantially between populations (Table 2). This variation was strongly associated with the interpopulational variation in mean LAG1 diameter (Spearman rank correlation coefficient between the two parameters, $r_s=-0.857$, $P=0.007$). As the mean LAG1 diameter tended to decrease with altitude in both species (Table 2), the LAG1 resorption frequency was lowest at the lowland locality and highest at moun-

TABLE 2. Percent of individuals with partial or complete resorption of the first two LAGs. Populations: *L. agilis* (1- Kostek, 2- Sergokala, 3- Khuchni, 4- Termenlik, 5- Kuli); *L. strigata* (11- Kostek, 12- Sergokala, 13- Khuchni).

| Population	Mean D_1(mkm)	LAG 1								LAG 2	
		Yearlings		Age 2+		Age >2+		All adults		All adults	
		%	n	%	n	%	n	%	n	%	n
1	600	0.00	17	21.43	14	26.09	23	24.32	37	2.70	37
2	461	0.00	4	75.00	24	88.89	9	78.79	33	6.45	31
3	530	4.76	21	62.50	24	100.00	8	71.88	32	0.00	32
4	422	4.55	22	87.50	8	100.00	21	96.55	29	0.00	29
5	432	0.00	2	83.33	6	100.00	15	95.24	21	0.00	21
11	541	0.00	10	33.33	21	52.38	21	42.86	42	0.00	37
12	445	-	0	63.16	19	50.00	8	59.26	27	0.00	27
13	458	12.50	16	77.78	18	100.00	16	88.24	34	0.00	34
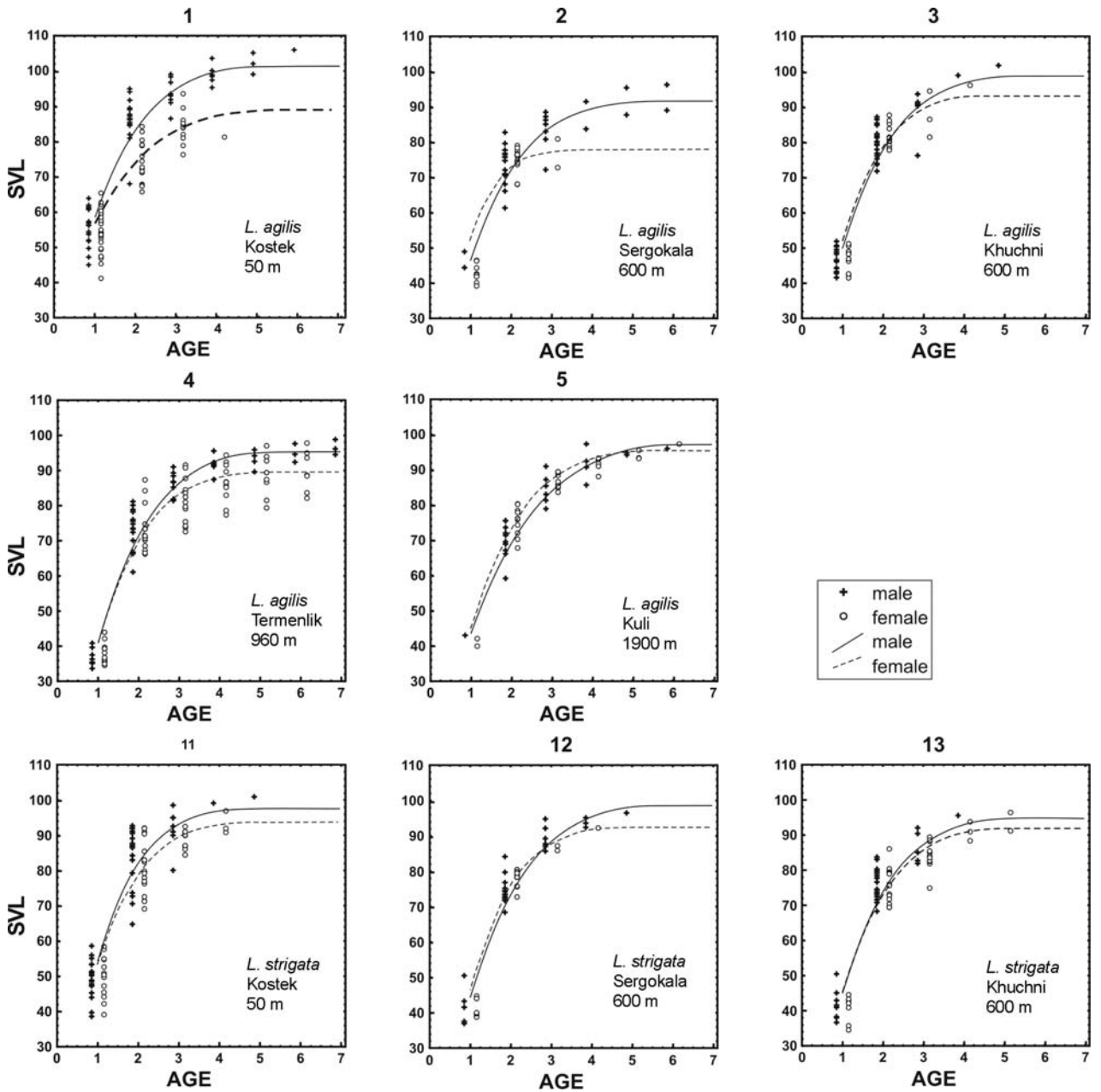
FIG. 3. Overall pattern of body growth in eight populations of *Lacerta agilis boemica* and *L. strigata.* Back-calculated SVLs (crosses, males; open circles, females) are plotted against age. Individual lizards occur more than once in this figure. Symbols for males and females are offset for clarity. Curves are best fit using the von Bertalanffy growth model. Locality elevations are given within the plots.

tain sites (Table 2). The resorption of LAG2 was extremely rare (Table 2) and no cases of resorption were revealed for the higher LAGs.

BACK-CALCULATED SVL

SVL at specific ages. Below we consider back-calculated snout-vent length (bc-SVL) at specific ages (the time of LAG formation in the femur) for lizards from the eight study populations. We assumed these SVLs to approximate the SVLs reached at the end of the corresponding activity seasons.

Back-calculated SVL at hatching (bc-SVL$_0$) was available for only a few individuals because the vast majority of the study specimens retained only a small (if any) portion of the neonate line in their femur bone. No sex and interlocality differences were found. Bc-SVL$_0$ was 30.4-37.2 (mean±SE: 34.5±0.39, n=20) for *L. a. boemica* and 32.6-35.9 (34.5±0.80, n=4) for *L. strigata.* These values are comparable with the data on hatchling SVL of the two taxa obtained in captivity by previous studies: *L. a. boemica*, Daghestan, 30-33 mm, n=23; *L. strigata*, Daghestan, 31-36 mm, n=29 (Roitberg, 1989); *L. a. boemica*, cf. Kabardino-Balkaria, 30-37 mm, n=37 (Warnecke, 2000); *L. strigata*, cf. Transcaucasia, 30-32 mm (Langerwerf, 1980).

Data on back-calculated SVLs at consecutive hibernations for the eight study populations (males and females separately) are compiled in Fig. 3. Following
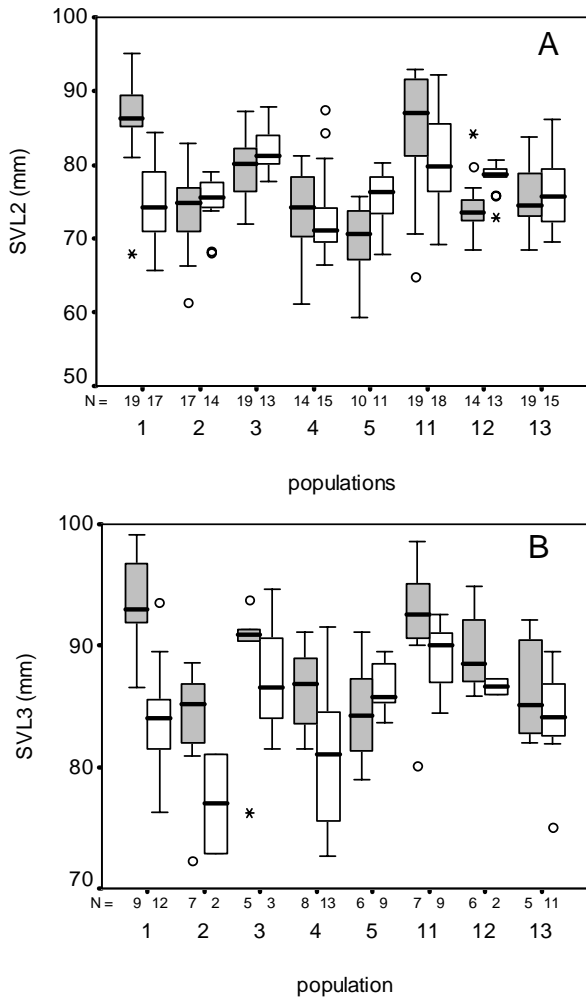
FIG. 4. Back-calculated SVL at the time of the second (A) and third (B) hibernation in *Lacerta agilis boemica* and *L. strigata* in the eastern North Caucasus. Populations: *L. agilis* (1- Kostek, 2- Sergokala, 3- Khuchni, 4- Termenlik, 5- Kuli) ; *L. strigata* (11- Kostek, 12- Sergokala, 13- Khuchni). The individual data are summarised as boxplots including the median (bold horizontal line), the 25th and 75th percentiles (box), range without outliers (vertical line), and outliers (observations located more than two interquartile ranges above or below the median) indicated as open circles or asterisks. Shaded figures are males and unshaded figures are females.

these data, the highest annual increment in SVL for all populations occurred between the 1st and 2nd hibernations (in yearlings) with progressively lower increments in subsequent activity seasons. Growth is, therefore, evidently asymptotic. Another related pattern is a clear separation between the SVL ranges of yearlings and adults (with the exception of the lowland population of *L. agilis* in which they nearly overlap) just at the beginning of the activity season (Fig. 3). Two samples (*L. strigata*, Sergokala and *L. agilis*, Kuli) showed only a small overlap between the 2-yr-olds and older animals, but in most populations these two age groups could not be identified by SVL.

Sex differences in SVL (sexual size dimorphism, SSD) showed the following patterns. No SSD was found for SVL at the first hibernation (bc-SVL$_1$). At the age of

the second hibernation, SSD differed between the populations: it was male-biased (males are the larger sex) for *L. agilis* from Kostek and female-biased for *L. agilis* from Kuli and *L. strigata* from Sergokala (Mann-Whitney test, $P=0.001$, $P=0.007$, $P=0.005$ for the respective single tests; $P<0.05$ after the Bonferroni adjustment for eight simultaneous tests; Fig. 4A). No female-biased SSD were found for older ages (Fig. 4B). As the age-size relationships in the study samples (Fig. 3) became effectively linear when Age was log-transformed, an ANCOVA with SVL as the dependent variable, ln(Age) as the covariate and Sex as the factor was performed for each population to check for SSD consistency. In two *L. agilis* populations the effect of Sex was significant (after Bonferroni adjustment, $P<0.001$ for Kostek and $P<0.05$ for Termenlik) indicating a consistent male-biased SSD in adult animals.

Bc-SVL$_1$ exhibited clear differences between the species; size distributions of *L. a. boemica* are shifted towards higher values from those of sympatric *L. strigata* (Fig. 5; Mann-Whitney test, $P<0.001$ for Kostek and Khuchni, $P=0.1$ for Sergokala). Within each species, mean and maximum SVL$_1$ in the lowland locality (Kostek) were higher than in the submontane localities (Sergokala and Khuchni); for both species the Mann-Whitney test provided $P<0.001$ for the Kostek/Sergokala and Kostek/Khuchni comparisons. In *L. a. boemica*, there were differences between the mountain population of Termenlik on one hand and all the lowland and submontane populations on the other (Mann-Whitney test, $P<0.001$ for all three comparisons), with no significant differences being detected between the two mountain populations, Termenlik and Kuli (Mann-Whitney test, $P=0.019$, $\alpha=0.05/10=0.005$ after the Bonferroni correction for multiple comparisons among 5 samples). Thus, SVL$_1$ decreased with elevation in both study species.

Unlike for bc-SVL$_1$, the between-species and among-population comparisons for bc-SVL$_2$ showed no clear trend with altitude. In *L. agilis*, the males and females clearly exhibited different patterns of interlocality variation (Fig. 4A), that reflected a pronounced interlocality variation in the pattern of SSD (see above). No sex differences in the pattern of interlocality variation were found for *L. strigata*.

For bc-SVL$_3$, the pattern of interlocality variation was similar to that of bc-SVL$_2$, and in both species males from Kostek tended to be larger than those from other localities (Fig. 4B).

Asymptotic size. Asymptotic SVL and growth constant of the von Bertalanffy growth model were calculated for male and female samples of the eight study populations (Appendix 2; see also Fig. 3 for corresponding growth curves). Following the conservative approach of Schoener & Schoener (1978) we considered the observed differences between sample estimates of growth curve parameters as significant only if their 95% confidence intervals did not overlap. Sample estimates of asymptotic SVL in males were higher than
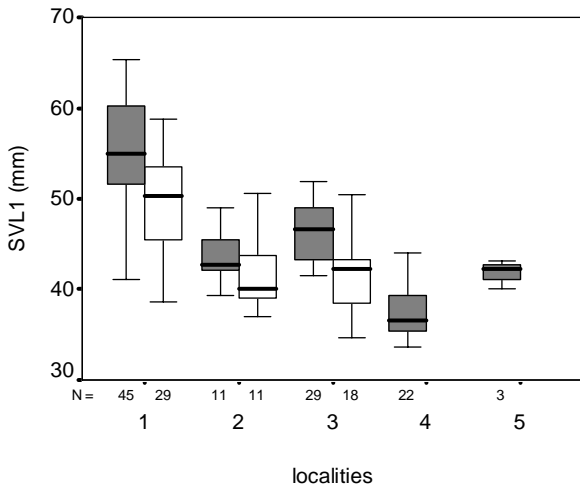
FIG. 5. Back-calculated SVL at the time of the 1st hibernation in *Lacerta agilis boemica* (shaded figures) and *L. strigata* (unshaded figures) from five localities in the eastern North Caucasus. Boxplots as in Fig. 4. Localities: 1- Kostek, 2- Sergokala, 3- Khuchni, 4- Termenlik, 5- Kuli.
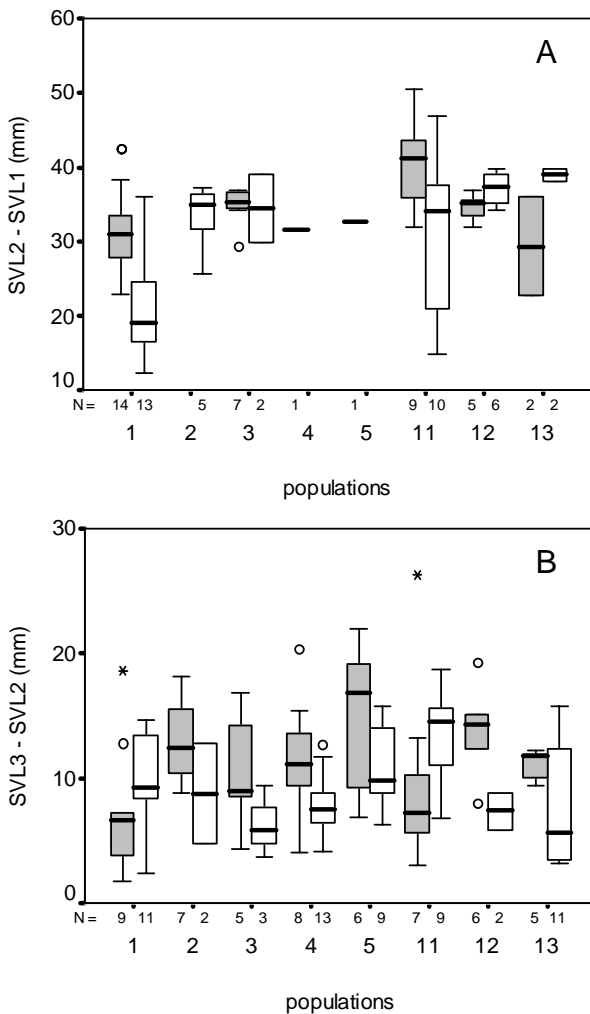

FIG 6. Individual annual increments of back-calculated SVL between the first and second hibernation (A) and between the second and third hibernation (B) in *Lacerta agilis boemica* and *L. strigata* in the eastern North Caucasus. Boxplots as in Fig. 4.

those of females in all eight populations (sign test: $P<0.01$). Sex differences were also significant in two individual populations: *L. agilis* from Sergokala and Termenlik. The largest magnitude of sex differences was found in samples of *L. agilis* from Kostek and Sergokala (Appendix 2).

On the whole, asymptotic SVL and characteristic growth rate exhibited no pronounced interpopulational differences. However, in both sexes, but especially in the females, *L. agilis* from Sergokala showed a lower asymptotic SVL than the other study populations (Appendix 2).

The 80th percentiles were in most cases rather similar to the asymptotes of the von Bertalanffy growth model (Appendix 2): in eleven of the sixteen study samples the difference between the two estimators varied from –2.1 to +1.6. In the other five samples, however, the absolute value of this difference ranged from 4.5-7.6. Like the asymptotes of the growth equation, the 80th percentiles were higher in males than in females (in seven out of the eight populations), with the largest sex differences found in *L. agilis* from Kostek and *L. strigata* from Sergokala (Appendix 2). Between populations, the 80th percentiles showed the lowest values in *L. agilis* from Sergokala as was the case for the asymptotes.

Annual increments in SVL. Back-calculating SVL from bone growth marks provided not only age-size data (Fig. 3), but also individual growth trajectories from which growth increments between consecutive hibernations can be computed. SVL increments between the first and second hibernations (SVL_2-SVL_1) which incorporated most of the growth in all study populations are summarised in Fig. 6A. In the lowland locality (Kostek) which provided appropriate sample sizes for all species/sex combinations (Fig. 6A), *L. strigata* tended to grow faster than the syntopic *L. agilis* (Mann-Whitney test, $P=0.020$ for males, $P=0.041$ for females), and the males grew faster on average than the females in both species (Mann-Whitney test, $P<0.001$ for *L.agilis*, $P=0.035$ for *L. strigata*). This pattern of differences also persisted if the effect of SVL_1 was statistically removed by use of the residuals of the linear regression of SVL_2-SVL_1 on SVL_1 (total data in Fig 6A) instead of the absolute SVL increments (Mann-Whitney test provided $P<0.05$ for all four comparisons). We employed these nonparametric tests because heterogeneity of variances in SVL_2-SVL_1 precluded use of GLM procedures.

For seven study samples, in which at least two specimens of unequal age possessed LAG1 and LAG2, Spearman rank correlation coefficient between SVL_2-SVL_1 and Age was computed. In all seven samples this correlation was negative (sign test: $P<0.05$), being significant in one sample (*L. strigata*, Kostek, females, r_s= -0.874, $P=0.001$).

SVL increments between the second and third hibernations (SVL_3-SVL_2) provided much larger samples than SVL_2-SVL_1 (Fig. 6B), and no heterogeneity of variances was found. ANOVA with SVL_3-SVL_2 as the dependent variable, and Sex, Locality, and Species as

the factors showed significant effects of Sex ($F_{1,76}$= 7.435, P=0.008) and Sex × Locality interaction ($F_{4,76}$= 3.733, P=0.007). All other factors and interaction terms were non-significant. In most populations the males tended to have higher growth increments than the females, but both species exhibited the opposite pattern in Kostek (Fig. 6B). However, just in Kostek, males grew faster than the females between the first and second hibernations (Fig. 6A).

An ANCOVA with SVL_3-SVL_2 as the dependent variable, SVL_2 as the covariate, and Sex, Locality and Species as the factors showed significant effects of the Covariate ($F_{1,76}$=71.10, P<0.001) and Sex ($F_{1,76}$=14.38, P=0.001) while all other sources were non-significant or marginally significant (P=0.036-0.069 for Locality and Species, P=0.138-0.612 for the interaction terms). Thus, the variation in SVL_2 cannot be solely responsible for the observed sex differences in body growth between the second and third hibernations. However, this variation might explain the deviating pattern of sex differences for SVL_3-SVL_2 in Kostek, because after correcting for SVL_2 (ANCOVA) Sex × Locality interaction was not any more significant.

DISCUSSION

AGE STRUCTURE

We believe the age structures of our study samples are, in general, representative for the whole populations. When specimens were collected, efforts were made to catch every individual of both species on the study sites until an appropriate sample size (25-30 specimens of each sex) had been achieved. Although some differential, age-related catchability cannot be excluded, we see no reason to suspect a substantial sampling bias, at least for adult animals.

In our lowland and submontane localities the age structure of both study species is characterised by a maximum age of 4-6 years and predominance of 2- and 3-yr-olds among adult individuals (Fig. 2). Similar age compositions were reported for several *L. agilis* populations in West Ukraine and South Siberia (reviewed in: Roitberg & Smirina, 1995) and most other medium-sized and smaller species of lacertid lizards studied so far (e.g. Orlova & Smirina, 1983; Smirina *et al.*, 1984; Castanet, 1994).

In contrast, in the mountain populations of *L. a. boemica* the maximum ages were 7-8 years, with 2- and 3-yr-old animals constituting some 50% of adults (Fig. 2). Comparable age structures were found in two North European *L. agilis* populations (Strijbosch & Creemers, 1988; Olsson & Shine, 1996).

The increase in longevity and mean age in the mountain populations as compared to their conspecifics from lower elevations (Fig. 2) has already been reported for various lizard species (Ballinger, 1979; Melkumyan, 1983; Roitberg & Smirina, 1995; Rohr, 1997; Wapstra *et al.*, 2001) and many amphibians (reviews in: Smirina, 1994; Miaud *et al.*, 2000). Like some other altitudinal

trends considered above, this pattern can be related to the length of activity season: shorter activity in cooler climate should reduce the risk of predation or other accidental death (Adolph and Porter, 1993; Ryser, 1996; Willemsen & Hailey, 2001). Additionally, Ballinger (1979) suggested that there could be lower predation pressure due to a reduced number of predator species in areas with colder climates which could explain the enhanced longevity in highland lizard populations. Although this may be the case for our study populations (the snake *Coluber caspius*, an effective predator of green lizards, does not occur in the two mountain sites, while it is rather common at lower elevations), the altitudinal differences in predator diversity are not as evident in our study as the differences in length of activity season.

Some features of interlocality variation revealed in this study differed from our expectations; (1) The lowland *L. agilis* population showed higher mean adult age than the submontane populations; (2) Although the altitudinal differences between Termenlik and the two submontane localities, Sergokala and Khuchni, are much lower than those between Termenlik and Kuli (Appendix 1), the *L. agilis* from Termenlik exhibited the same (if not a higher) mean age and longevity as their high-mountain conspecifics in Kuli (Fig. 2). We have no hypothesis to explain pattern 1; the pattern is minor in any case when compared to the differences between lowland and submontane populations on one side and mountain populations on the other. Pattern 2 can be related to certain climatic characteristics of Termenlik (precipitation, evaporation, number of days with mean air temperature above 10°C – Appendix 1) which would make the overall time of lizard activity comparable to that of the highlands. It seems, it is the length of activity season that determines the main trend under discussion, and populations living in colder environments would exhibit higher mean age and longevity irrespective of altitude (e.g., Saint Girons *et al.*, 1989). Similarly, a *Timon lepidus* population from a hot region, where the annual activity was reduced by aestivation, showed higher mean age than a population living in a cooler and mesic environment (Mateo & Castanet, 1994).

PATTERN OF LAG RESORPTION AND POSSIBLE BIAS IN BACK-CALCULATED DATA

Partial or complete loss of LAG1 due to endosteal resorption generally did not disturb age determination as there was only a small overlap between the distribution of marrow cavity diameters and the distribution of D_1 in the study samples. However, this resorption is a serious problem for growth inference from skeletochronological data as it precludes measuring the corresponding ring diameters (D_i) and back-calculating the corresponding SVLs. A high resorption frequency not only reduces the amount of data, but may also bias our estimations of mean values of ring diameters. For merely mechanical reasons, growth rings with smaller diameters are expect-

TABLE 3. LAG1 diameter in different age-sex groups within populations. Only the Population/Sex combinations with $n>1$ for both age groups were considered. Diff=Mean of Adults - Mean of Yearlings.

Populations (as in Fig. 2)	Sex	Yearlings (Age=1+)			Adults (Age >1+)			Diff.
		Mean	SD	n	Mean	SD	n	
1	m	0.667	0.017	5	0.611	0.061	14	-0.056
	f	0.588	0.058	12	0.574	0.077	14	-0.014
2	f	0.442	0.022	2	0.451	0.028	7	0.009
3	m	0.531	0.038	9	0.535	0.045	7	0.004
	f	0.528	0.028	11	0.516	0.066	2	-0.012
11	m	0.561	0.052	7	0.545	0.084	9	-0.016
	f	0.518	0.087	3	0.531	0.067	10	0.013
13	m	0.460	0.035	6	0.527	0.088	2	0.067
	f	0.459	0.016	8	0.379	0.002	2	-0.080

ed to be destroyed more frequently than larger rings. Thus, the mean D_1 (and body length at the first hibernation) might be slightly overestimated (*cf*. Ryser, 1996). Such a bias in the size distribution of a growth mark might be called pseudoselection because it is obviously unrelated to size-dependent survival (true natural selection), but under a high resorption frequency it may imitate true natural selection with a higher survival rate for larger juveniles. The latter was reported for two frog species in which the mean D_1 of adults was higher than that of young animals under a low resorption frequency (Esteban *et al*., 1999; Esteban & Sanchiz, 2000). The pronounced negative correlation between the resorption frequency and mean diameter of D_1, found for the variation between populations (Table 2), seems to be in line with our pseudoselection hypothesis. At the same time, no consistent trend was revealed in comparisons of the mean D_1 between adults and yearlings within populations (Table 3). Possibly, the proposed pseudoselection can be compensated by other factors which affect the rate of endosteal resorption.

EVALUATION OF THE BACK-CALCULATED DATA

Virtually all body growth data in this study were obtained with the back-calculation technique which had not previously been applied to squamate reptiles. Although no other data on SVL growth were available for our study populations, some indirect validation of back-calculated SVL values can be made. For both species, back-calculated SVLs at hatching (this study) were located within the range of values obtained in captivity (Langerwerf, 1980; Roitberg, 1989; Warnecke, 2000). This correspondence is very important because the highest errors of back-calculation are expected just for lowest values of D_i and SVL_i (Marunouchi *et al*., 2000).

For SVL at the end of the first and subsequent growth seasons, we compared back-calculated and field data by maximum values (in fact we used the two largest values to reduce variation by chance; we did not use upper per-

centiles here because it was difficult to appropriately delimit the sample for our field data). Maximum values should be less sensitive to pseudoselection and to other sources of sampling bias (e.g. a proportion of individuals whose growth rate or activity was reduced due to temporal or local effects) than the means or medians. As SVL distributions were effectively continuous, maximum SVLs at specific ages are expected to manifest the body growth potential of a given population in a particular environment and should therefore be biologically meaningful.

The largest values of back-calculated SVL at the first hibernation recorded in our lowland site (Kostek) were 64-65 mm in *L. agilis* and 58-59 mm in *L. strigata*. In large juvenile samples caught in September-October 1981-1984 in another lowland locality (Makhachkala, ca. 100 km SE from Kostek, a mark-recapture study) the largest values were 61-63 mm for *L. agilis* and 54-55 mm for *L. strigata* (Roitberg, 1989).

The largest back-calculated SVL at the second hibernation in the lowland locality was 94-95 mm in *L. agilis* and 92-93 mm in *L. strigata*. In Makhachkala, some *L. agilis* yearlings could reach 87-90 mm in August – September of their 2nd activity season (E. S. Roitberg, unpublished data), and one yearling *L. strigata* from Kostek had a SVL of 92 mm on 7 Sept. 1984.

Even though a slight overestimation of SVL for the young ages might be suspected, the overall conformity between back-calculated and comparable field data considered above suggests the former to be suitable at least for rough estimations. Additional support for the plausibility of our back-calculated data can be seen in the validation study on *Rana japonica* (Marunouchi *et al*., 2000, see our Methods section). At least, the correlation between body length and bone thickness in our study samples was as high as that in *R. japonica*, and the femur growth is expected to be even more integrated in the body growth than that of a phalanx. However, validation studies on lizards are necessary to reliably estimate the

mean and range of possible deviations of our back-calculated data from actual values.

Sergeev (1937) used the Dahl-Lea formula for back-calculating age-specific body lengths from carapace growth rings in several turtle species. Like our study, he reported conformity of back-calculated data with direct measurements on young individuals of known age (but see Wilson *et al.*, 2003 for concerns about use of carapace growth rings as recording structures).

PATTERNS OF VARIATION IN AGE-SPECIFIC SVLS AND ANNUAL SVL INCREMENTS

The back-calculation procedure provides estimations of individual body size at ages before capture, thus multiplying the total amount of age-size data, especially for older animals. It estimates the body size at specific ages, just at the end of a growth season (or at the beginning of the next one), providing comparable data from samples collected at different times of the season.

The decrease of mean and maximum body length at the 1st hibernation (SVL_1) with altitude can be explained by the differences in the time available for growth. In the mountains, juveniles hatch later and go into hibernation earlier than those in low-elevation sites. Lower mean SVL_1 in *L. strigata* as compared to the syntopic *L. agilis* can be explained in the same way: *L. strigata* hatched later in the season (Roitberg, 1989; E. S. Roitberg, unpublished data) due to a longer incubation time (Zakharov *et al.*, 1982).

In the lowland populations of both species, the largest juveniles enter their first hibernation and, as yearlings, start their second activity season with a SVL of 60-65 mm (Fig. 3, Fig. 5). Minimal SVL at the first reproduction in lowland Daghestan was estimated as 70 mm (Khonyakina, 1970; see also Tertyshnikov, 2002 for an adjacent region). In our lowland site, about 50% of yearling *L. agilis* and a few yearling *L. strigata* captured in the first half of June were 70-77 mm in SVL. Five of them (four female *L. agilis* and one female *L. strigata*) had oviductal eggs so in lowland Daghestan, some yearling females of the study species do reproduce. This finding is noteworthy because even for warm climate regions an age of maturity at 22-23 months was previously reported for both study species (Muskhelishvili, 1970; Khonyakina, 1970, 1972; Darevskij, 1984; Tertyshnikov, 2002), except *L. strigata* from south-western Turkmenistan for which the reproduction of yearlings was reported (Shammakov, 1981). No yearling females with oviductal eggs were found in the study samples from the submontane and mountain sites (E. S. Roitberg, unpublished data). We believe that the proportion of reproducing female yearlings may be substantial in our lowland locality (at least in *L. agilis*), it is rather small in our submontane localities, and no yearlings reproduce in the mountain sites. A similar shift in age of maturity in colder climates has been shown for many lizard species (Ballinger, 1979; Heulin, 1985; Rohr, 1997; Wapstra *et al.*, 2001; but see Grant & Dunham, 1990 for an opposite shift in age at maturity at high elevation).

The proposed altitudinal differences in the mean age at first reproduction in the study species agree with the model of Adolph & Porter (1996) which views variation in age and size at maturity in lizards as a product of the proximate effect of temperature on their growth and maturation pattern. Individuals living in warmer areas are predicted to mature earlier (at a relatively small size), whereas their conspecifics from cool environments delay maturity (and thus invest available energy to further growth) because they cannot reach an appropriate size by the time at which reproduction is still suitable. This proposal might also explain some patterns of variation in age-specific SVL and annual growth increments revealed in this study if we assume that the energetic costs of reproduction are considerably higher in females than in males (Nagy, 1983; Anderson & Vitt, 1990).

In the lowland locality, males grew rapidly between the first and second hibernations in both species (Fig. 6A). By their third activity season, many of the males become quite large (some individuals of both species can exceed 90 mm in SVL that corresponds to some 90% of their final size – Fig. 4A), and their further growth slows down (Fig. 6B) as they approach their final (asymptotic) body length. In the hot and dry climate of the Ararat valley in Armenia, *L. strigata* can also approach final SVL at the time of entering the 2nd hibernation (Melkumyan, 1983). Lowland females exhibited much lower SVL increments in their second activity season than the males, particularly in *L. agilis* (Fig. 4A, Fig. 6A), probably because a substantial proportion of them did reproduce and allocated plenty of energy to egg production at the expense of body growth. At higher elevations, the study species exhibited no sex differences in body growth between the first and second hibernations (Fig. 4A, Fig. 6A), but during the following season the females grew less intensively than the males (Fig. 6B). It seems, the phase of lower body growth in females relative to males, being associated with the first reproduction, is merely shifted in the lowland locality to younger ages, because the warmer climate (Appendix 1) accelerates growth and maturation (Adolph & Porter, 1996). A lower growth rate of young reproducing females relative to males of the same age was reported for various lizard species (e.g., Anderson & Vitt, 1990; Howland, 1992; Rocha, 1995).

ASYMPTOTIC SIZE

For species with asymptotic growth after maturity, asymptotic size is affected by a much shorter list of proximate factors than average size (Stamps, 1993). Therefore, for comparative studies focusing on differences among populations or between sexes, asymptotic size is preferable to mean adult size (Stamps & Andrews, 1992; Stamps, 1993; Brown *et al.*, 1999).

There are some problems with estimating the mean asymptotic size from growth equations using nonlinear regression. Like the slope and intercept of a linear regression, the parameters A (asymptote) and k (characteristic growth rate) of a growth equation are es-

timated simultaneously. Their statistical estimates are thus not independent from one another and any factor that affect estimates of k can also influence estimates of A (Stamps *et al.*, 1994). Therefore, a deficiency of old, full-grown individuals or a strong variation in the proportion of young, small animals in a particular sample might bias the considered estimates (James, 1991; Stamps *et al.*, 1994). This is a probable explanation for the extremely high k and low A in female *L. agilis* from Sergokala (Appendix 2) because this sample included many data points for age 1 while only one data point for ages higher than 2 (Fig. 3).

Furthermore, through the use of group data (a composite of points of individual growth curves) to model individual growth, the resulting growth curve can be biased by differential survival of fast-growing and slower-growing individuals (Mina & Klevezal, 1976; Bruce *et al.*, 2002). The latter phenomenon, in the form of a lower survival of fast-growers, has been reported for a range of lizard species (Smirina & Tsellarius 1996; Sorci *et al.* 1996; Olsson & Shine, 2002). The negative correlation between the individual age at capture and the SVL increment between the first and second hibernations revealed in the present study may similarly indicate a lower survival of fast-growing animals as compared to those with lower growth rate. If this bias is moderate in magnitude or, at least, does not differ substantially between populations, cautious use of growth curves for comparative purposes seems suitable.

The 80th percentile suggested as an alternative estimator of mean asymptotic SVL (Brown *et al.*, 1999) is likely to be resistant to any variation outside the upper area of character distribution; it is also not sensitive to outliers. However, if the proportion of full-grown individuals is very low (due to a sampling bias or a low survival of older animals) this estimate may be even more biased than the estimate of A from the growth equation.

We believe that if the two estimators of asymptotic size, which are unrelated statistically and calculated from different sets of data (back-calculated SVLs for the growth-based estimator and SVLs at capture for the percentile), provide comparable values and similar patterns of variation, these are likely to be biologically meaningful. Viewing our results (Appendix 2) in this way we can state that in the study populations, males tend to have larger final size than females, but the extent of the differences varied between populations, being rather large (11-12 mm for the different estimators) in *L. agilis* from Kostek and quite small (0-3 mm) in *L. agilis* from Kuli. The only clear pattern of the interpopulational differences is a lower final size of *L. agilis* from Sergokala. Apart from a true geographic variation in adult SVL (e.g., Saint Girons *et al.*, 1989; Mateo & Castanet, 1994), this pattern might also result from an interannual fluctuation in age structure or growth rate because the whole study sample was collected during a few days of a single season (Table 1).

SEXUAL SIZE DIMORPHISM (SSD)

A pronounced male-biased SSD found for adult *L. agilis* SVL in a few study sites is noteworthy because virtually all other *L. agilis* populations studied thus far exhibited either a female-biased SSD or no obvious sex differences for SVL (see e.g. Olsson & Shine, 1996; Amat *et al.*, 2000 for West Europe; see Darevsky *et al.*, 1976 for more eastern parts of the species range).

Modern theory views SSD as a complex phenomenon, an outcome of several interacting factors (e.g. Shine, 1990; Stamps, 1993; Braña, 1996; Cox *et al.*, 2003). The most prevalent explanation for male-biased SSD in reptiles is intrasexual selection which favours larger males as they are generally more successful in male combat (e.g. Anderson & Vitt, 1990; Cox *et al.*, 2003). We can hypothesise that in *L. agilis* the intensity of this selection differs between subspecies or geographic regions (e.g. due to some differences in territoriality or other aspects of social behaviour; *cf.*: Shine & Fitzgerald, 1995) resulting in adaptive divergence in the SSD pattern. As was recently shown, intraspecific SSD variation in lizards can have an evolutionary component (Zamudio, 1998). A pronounced morphological (Roitberg, 1987) and genetic (Kalyabina *et al.*, 2001) separation of *L. a. boemica* from the rest of the species could argue for a phylogenetic determination of the distinctive male-biased SSD. However, phylogenetic determination can hardly explain the pronounced microgeographic variation of SSD pattern within *L. a. boemica*.

Apart from selective pressures, SSD may be influenced by proximate factors and reflect local, environmentally-induced variation in growth, maturation and survival rates (Shine, 1990; Stamps, 1993; Watkins 1996). This is especially true for reptiles and other animals whose body growth continues asymptotically after sexual maturity (Stamps, 1993). Taking into account that the different estimators of adult body length generally showed the strongest SSD in the lowland *L. agilis* population, we believe microgeographic variation for SSD within *L. a. boemica* is largely determined by proximate factors related to the length of activity season. According to theoretical predictions (Adolph & Porter, 1996; see above) and data on altitudinal variation of various reptile species (e.g. Ballinger, 1979; Rohr, 1997; Wapstra *et al.*, 2001), lizards from the lowland locality are expected to have a smaller average size at maturity than their conspecifics from higher elevations. In many reptiles the size at maturity was shown to strongly correlate with the final size (Andrews, 1982; Shine, 1990; Stamps *et al.*, 1998). As reproduction is expected to more strongly inhibit body growth in females than in males, earlier maturation might be responsible for smaller female body length and the consequently male-biased SSD in the lowland populations. An additional reason for smaller female size in warmer climates may be higher annual reproductive expenditures because in such an environment many females

produce two clutches per season (Baranov *et al*., 1976; Khonyakina & Ferkhatova, 1977). These hypotheses should be tested through further research to better evaluate proximate and evolutionary causes for geographic variation of SSD in *L. agilis*.

COMPARISONS BETWEEN THE STUDY SPECIES

L. a. boemica and *L. strigata*, two closely related species occupying the same environment, were compared for several age-specific SVLs and annual growth increments, asymptotic SVL, and age composition. Compared with *L. a. boemica*, *L. strigata* is characterised by longer egg incubation and later hatching time. Consequently, before and soon after their first hibernation, juvenile *L. strigata* are on average smaller than juveniles of the syntopic *L. a. boemica* (Fig. 5). However, at least in the lowland site, yearling *L. strigata* grew faster than those of *L. a. boemica* (Fig. 6A), so no substantial differences in SVL between the study taxa could be detected after the second hibernation (Fig. 4). These differences conform to the pattern of spatial distribution of the study species in the eastern North Caucasus: *L. strigata* occupies a much larger range of lowland localities than *L. a. boemica*, but the latter expands substantially further in the mountains (Roitberg *et al*., 2000).

Unlike other life-history studies comparing two related syntopic lizard species (Tinkle & Dunham, 1986; Strijbosch & Creemers, 1988) we revealed no differences in age composition. This might be attributed to closer relatedness between our study taxa which are not merely congeneric but belong to the same subgenus (Arnold, 1989). Another probably even more relevant difference from the above investigations is that our study taxa have similar adult sizes. Adult size was shown to be the major determinant of variation for the other life-history and demography traits among related lizard species (Dunham *et al*., 1988; Bauwens & Diaz-Uriarte, 1997; Molina-Borja & Rodríguez-Domínguez, 2004).

FINAL REMARKS

Much of the variation for age structure, body growth and sexual size dimorphism revealed in *L. a. boemica* and *L. strigata* along an altitudinal gradient in the eastern North Caucasus can be related to the length of activity season in line with the models of Adolph & Porter (1993, 1996). These models offer proximate explanations for the trends of life-history variation along environmental gradients that were previously considered as unequivocal adaptations (e.g., Ballinger, 1983; Dunham *et al*., 1988). Although several experimental studies revealed a genetic (population-specific) component of the interpopulational variation for growth rates in lizards (Ballinger, 1979; Ferguson & Brockman, 1980; Ferguson & Talent, 1993; Niewiearowski & Roosenburg, 1993), some recent studies with a powerful design could identify only the environmental sources of

such variation (Sorci *et al*., 1996; Qualls & Shine, 2000; Lorenzon *et al*., 2001). The latter was therefore treated as phenotypic plasticity within the reaction norm (Gotthard & Nylin, 1995). Obviously, not only the patterns of intraspecific life-history variation in lizards are diversified but also the extent to which they are genetically fixed. The progress in our understanding this diversity is primarily determined by intensive mark-recapture and experimental studies of model species. However, such studies can cover only a small portion of taxonomical and ecological diversity of situations which deserve to be investigated. Skeletochronology can substantially extend the range of the study populations because valuable data on individual age and growth can be obtained during a relatively short time. Our report has shown that much ecologically relevant data, which would otherwise require a long-term field study, can be obtained from museum samples if they are large enough and appropriately collected (the amount of data could be even greater if the resorption frequency of younger LAGs had not been so high). The back-calculation method proved to be a promising tool to extract quantitative data on lizard body growth from skeletochronological records.

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APPENDIX 1. Geographical and climate characteristics of the study sites. Except Sergokala, there are no meteorological stations near the study sites, so only rough estimations of climate parameters drawn from coarse climatological maps (Atlas of the Daghestan ASSR, 1979) were possible. Inequalities show the position of a study site between two adjacent isolines of the corresponding climate parameter.

Locality	Geographical coordinates	Altitude (m)	Precipitation (P) April -October, mm	Annual evaporation (E), mm	Annual no. days with t>10°C (N)	Mean t of July (°C)
1. Kostek	43°20'N, 46°46'E	ca. 50	ca. 250	800<<E<1000	180<N<200	24
2. Sergokala	42°28'N, 47°42'E	550	ca. 300	800<E<1000	180<N<<200	22
3. Khuchni	41°57'N, 47°57'E	600	ca. 300	700<<E<800	ca.180	20<t<<24
4. Termenlik	42°25'N, 47°00'E	960	ca. 500	600<<E<700	140<<N<<180	16<<t<20
5. Kuli	42°01'N, 47°15'E	1900	500<P<600	600<E<700	140$\leq$N<180	12<t<16

APPENDIX 2. Asymptotic SVL (A) and growth constant (k) of the von Bertalanffy growth model, and 80th percentiles of SVL (P80) of adult individuals for *Lacerta agilis boemica* and *L.strigata* from eight populations in the eastern North Caucasus. *The number of age-size values (data points in the scatter plots of Fig. 2); ** estimate ± asymptotic standard error; *** the number of adult (2-and-more years old) animals.

Study samples species	locality	sex	N*	A**	k**	R^2	n***	P80
agilis	Kostek	M	57	100.81±1.83	1.12±0.13	0.926	19	100.0
agilis	Kostek	F	55	89.12±5.00	0.88±0.27	0.839	17	88.0
agilis	Sergokala	M	32	91.51±2.36	0.97±0.12	0.815	17	90.0
agilis	Sergokala	F	25	77.11±2.55	2.76±1.22	0.963	14	83.8
agilis	Khuchni	M	42	98.50±3.29	1.00±0.13	0.947	19	94.0
agilis	Khuchni	F	30	92.24±2.71	1.46±0.23	0.966	13	91.0
agilis	Termenlik	M	48	95.22±1.08	0.97±0.06	0.967	14	97.0
agilis	Termenlik	F	70	89.04±1.17	1.10±0.10	0.925	15	94.2
agilis	Kuli	M	24	98.41±2.85	0.70±0.08	0.905	10	96.8
agilis	Kuli	F	33	95.36±1.12	0.96±0.06	0.957	11	97.0
strigata	Kostek	M	44	96.89±3.77	1.33±0.28	0.884	19	99.0
strigata	Kostek	F	43	93.01±3.03	1.26±0.24	0.889	18	92.4
strigata	Sergokala	M	29	98.82±2.64	0.86±0.09	0.956	14	96.0
strigata	Sergokala	F	22	91.61±2.01	1.31±0.12	0.986	13	84.0
strigata	Khuchni	M	33	94.55±3.90	1.02±0.16	0.940	19	89.0
strigata	Khuchni	F	41	91.39±1.95	1.12±0.12	0.951	15	92.0